Annals
of the
Missouri Botanical Garden

Vol. 40 MAY, 1953 No. 2

A CONTRIBUTION TO THE LICHEN FLORA OF ARIZONA AND NEW MEXICO

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The lichen flora of the states of Arizona and New Mexico is much less known than that of many other sections of the United States. In addition to the references on distribution given in the standard works of Tuckerman (1882, 1888) and Fink (1935), there are only scattered papers in the literature which are concerned with the lichens of these states. Tuckerman, in 1860 and 1862, reported on the collections made by Fendler near Santa Fe. When these records were brought together in 1866, several collections made by Wright in New Mexico were added. Tuckerman (1878) also wrote up some Arizona collections made by the U. S. Geological Survey of the 100th Meridian. It was not until some time later that Fink (1909, 1909a) studied the lichens of the vicinity of Tucson, Arizona, from where some new species were described by Zahlbruckner (1908, '09). In 1932 Bouly de Lesdain published an account of lichen collections from the vicinity of Las Vegas, New Mexico, made by Brother Arsène Brouard, and, in 1942, on further collections from the vicinity of Santa Fe. Magnusson (1929, 1937) treated the *Acarospora* of Brother Arsène Brouard. Herre (1944, 1950) has provided additional information on the lichen flora of New Mexico from San Miguel and Sierra counties. Finally, Darrow (1950) has reported on the arboreal lichen flora of southeastern Arizona. The present paper includes forms from some new localities in Arizona and New Mexico of which three are new species and a number are additions to the flora.

This compilation is the result of a study of two collections: (1) that of Dr. Robert A. Darrow made in various localities in southeastern Arizona in 1933 and 1934, and in the 1940's which includes only saxicolous and terricolous forms; (2) that made by Mr. and Mrs. Francis Elmore at Chaco Canyon National Monument in northwestern New Mexico in 1952. The latter is for the most part saxicolous, but a few corticolous forms are included. Thus most of these lichens are crustaceous rock-inhabiting ones which form a conspicuous element in the vegetation of these arid mountainous regions.

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The arrangement and nomenclature, wherever possible, follows that of Fink (1935). The treatment of *Acarospora* is in accord with that of Magnusson (1929a). A complete set of specimens is on deposit in the herbarium of the Missouri Botanical Garden.

I should like to thank Dr. Carroll W. Dodge for his valuable guidance and assistance throughout this study.

LIST OF SPECIES

VERRUCARIA FUSCELLA (Turn.) Ach.—ARIZONA: Tucson, on caliche, 2500 ft., Dec. 4, 1933, *Darrow 572;* Tucson Mts., on volcanic rock, 3000 ft., March 11, 1934, *Darrow 746.* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16 & 20, Feb. 28, 1952, *Elmore.*

STAUROTHELE UMBRINA (Ach.) Tuck.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *Elmore.*

DERMATOCARPON POLYPHYLLUM (Wulf.) Dalla Torre & Sarnth.—ARIZONA: Pima Co., Rincon Mts., on shale, 4500 ft., March 4, 1934, *Darrow 697.*

DERMATOCARPON RUPICOLA Zahlbr.—ARIZONA: Tucson Mts., on andesite, 3500 ft., March 15, 1934, *Darrow 690.*

ENDOCARPON PUSILLUM Hedw.—ARIZONA: Tucson Mts., on caliche, 3000 ft., March 11, 1934, *Darrow 745.*

ARTHOPYRENIA HALODYTES (Nyl.) Arn.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

PYRENULA NITIDA (Weig.) Ach.—NEW MEXICO: Chaco Canyon, on greasewood *(Sarcobatus vermiculatus* (Hook.) Torr.*)*, 6200 ft., Jan. 20, 1952, *Elmore.*

URCEOLARIA SCRUPOSA (Schreb.) Ach. var. BRYOPHILA (Ehrh.) Ach.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on *Cladonia* primary thalli, Dec. 24, 1933, *Darrow 537.*

LEPTOGIUM APALACHENSE Nyl.—ARIZONA: Pima Co., Rincon Mts., on shale, 4500 ft., March 4, 1934, *Darrow 698.*

LEPTOGIUM BURGESSII (L.) Mont.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on soil, Dec. 24, 1933, *Darrow 533.*

PLACYNTHIUM MICROPHYLLIZUM (Nyl.) Hasse—ARIZONA: Tucson, on soil, 2500 ft., Nov. 26, 1933, Apr. 5, 1934, *Darrow 527, 691;* Pima Co., Cortaro, on soil, 3000 ft., Nov. 26, 1933, *Darrow 528;* Pima Co., Rincon Mts., on soil, 3500 ft., March 4, 1934, *Darrow 740, 741.*

LECIDEA BRANDEGEI Tuck.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

LECIDEA PARASEMA Ach.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

LECIDEA PLANA (Lahm) Nyl.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

LECIDEA VORTICOSA (Floerke) Koerb.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

RHIZOCARPON DISPORUM (Naeg.) Müll. Arg.—ARIZONA: Mt. Lemmon, Santa Catalina Mts., on marble, 8500 ft., April 1, 1934, *Darrow 721*.

ACAROSPORA AMERICANA H. Magn.—ARIZONA: Tucson Mts., on volcanic rock, March 11, 1934, *Darrow 747;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore*.

ACAROSPORA COLORADINA H. Magn.—ARIZONA: Tucson Mts., on volcanic rock, 3000 ft., March 11, 1934, *Darrow 746*.

ACAROSPORA OXYTONA (Ach.) Mass.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *Elmore*.

ACAROSPORA PELTASTICA Zahlbr.—ARIZONA: Tucson Mts., on volcanic rock, 3000 ft., March 11, 1934, *Darrow 736;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *Elmore*.

ACAROSPORA STRIGATA (Nyl.) Jatta—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16 & 20, 1952, *Elmore*.

ACAROSPORA TENEBRICA H. Magn.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore*.

ACAROSPORA WASHINGTONENSIS H. Magn.—ARIZONA: Pima Co., Rincon Mts., on schist, 4500 ft., March 4, 1934, *Darrow 788*.

PERTUSARIA FLAVICUNDA Tuck.—ARIZONA: Santa Rita Mts., on igneous rock, 7200 ft., Aug. 14, 1934, *Darrow 820*.

LECANORA ATRA (Huds.) Ach.—ARIZONA: Patagonia Mts., on granite, 5500 ft., Oct. 6, 1946, *Darrow 4252*.

LECANORA CENISIA Ach.—ARIZONA: Santa Rita Mts., on igneous rock, 7000 ft., July 16, 1934, *Darrow 796*.

LECANORA CONTORTA (Hoffm.) Stiz.—ARIZONA: Mt. Lemmon, Santa Catalina Mts., on quartz, 8500 ft., April 1, 1934, *Darrow 724*.

LECANORA DIFFRACTA Ach.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on granite, 6500 ft., Dec. 24, 1933, *Darrow 470*.

LECANORA (ASPICILIA) **elmorei** E. Rud., var. nov.—TYPE: NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 20, 1952, *T. & F. Elmore*.

Thallus determinatus, laevigatus, obscure olivaceus, areolatus, areolis crassis convexisque, 1–2 mm. diametro; cortex 31–41 μ crassitudine, K—, fastigiatus, dimidia parte corticis crassitudine strato gelifacto tectus, hyphis circa 3 μ diametro; algae ad *Trebouxiam* pertinentes, cellulis ad 38 μ diametro, in strato non continuo, 100–170 μ crassitudine sub cortice; medulla hyphis laxe contextis circa 4 μ diametro. Apothecia in areolis crassioribus immersa, unum vel plura in quavis areola, amphithecio prominente, persistente, crasso, thallo concolore, disco concavo obscure olivaceo-alutaceo pulverulento; hypothecium indistinctum sed densum; thecium 150–171 μ altitudine; paraphyses simplices, septatae, circa 2 μ diametro, apicibus clavatis; asci 71.5–100.0 $\times$ 14.3–15.7 μ, clavati, apicibus incrassatis; sporae uniseriate, 3–4-nae, sphaericae, 17.4–24.4 μ diametro, granulosae, episporis tenuibus.

Thallus determinate, smooth, deep olive, closely areolate, the areolae thick and convex, 1–2 mm. in diameter; cortex fastigiate, 31–41 μ thick, covered by a

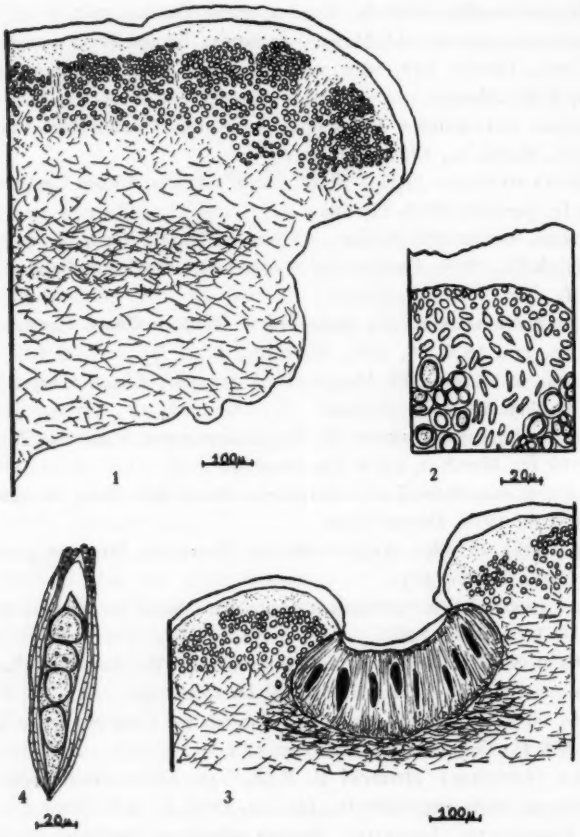

Fig. 1. *Lecanora elmorei* E. Rud.

1. Section of thallus.
2. Enlarged section showing cortex.
3. Section of an apothecium.
4. Ascus with associated paraphyses.

gelatinous layer about half the thickness of the cortex, KOH—, the hyphae approximately 3 μ thick; algae *Trebouxia,* forming a layer 100–170 μ thick below the cortex, broken into vertically rectangular patches separated by fungous hyphae, the cells globular to slightly angular, 10–38 μ in diameter; medulla of loosely woven hyphae about 4 μ in diameter. Apothecia sunken, the margin formed of the remaining part of the aerolae, one to several per areolae, the disc very concave, dark olive-buff, appearing powdery; margin persistent, raised and thick, thalline, colored like the thallus; epithecium of gelatinous tips of paraphyses; hypothecium indistinct, slightly denser than the underlying tissues; thecium 150–171 μ thick, the paraphyses simple, filiform, septate, about 2 μ thick, the tips swollen. Asci clavate, 71.5–100.0 $\times$ 14.3–15.7 μ wide, hyaline tips present in many; spores uniseriate, 3–4 per ascus, globose, 17.4–24.4 μ in diameter, mostly coarsely granular, the epispores thin.

This new species is easily distinguished by its 3–4 globose spores per ascus and by having *Trebouxia* as its alga. The globose-spored species *Lecanora praecrenata* Nyl., with its diffuse, whitish, indeterminate thallus and sessile brown apothecia, contrasts easily with the thick, closely areolate, deep-olive thallus and sunken apothecia of the present species.

LECANORA EPULOTICA (Ach.) Leighton—ARIZONA: Santa Rita Mts., on igneous rock, 6500 ft., July 1, 1934, *Darrow 814.*

LECANORA FRUSTULOSA (Dicks.) Ach.—ARIZONA: Carr Canyon, Huachuca Mts., on marble, 5600 ft., June 12, 1945, *Darrow 4236.*

LECANORA MELAENA (Hedlung) Fink—ARIZONA: Tucson Mts., on calcareous rock, March 25, 1934, *Darrow 682.*

LECANORA PARISENSIS Nyl.—NEW MEXICO: Chaco Canyon, on greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.), 6200 ft., Feb. 28, 1952, *Elmore.*

LECANORA POLYTROPA (Ehrh.) Rabh.—ARIZONA: Santa Rita Mts., Pima Co., on igneous rock, 4500 ft., Aug. 14, 1934, *Darrow 819.*

LECANORA THAMNOPLACA Tuck.—ARIZONA: Santa Rita Mts., on igneous rock, 7000 ft., Aug. 14, 1934, *Darrow 822;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

PARMELIA NOVO-MEXICANA Gyeln.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

CALOPLACA **arizonica** E. Rud. sp. nov.—TYPE: ARIZONA: Cortaro, on rhyolite, 3000 ft., Nov. 26, 1933, *R. A. Darrow 521.*

Thallus areolatus, fuscus; areolae 0.5–1.0 mm., dispersae; cortex circa 18 μ, fastigiatus, strato gelifacto tectus, K obscure purpurascens; algae protococcoideae ad 10 μ diametro, cellulis sphaericis vel subangulosis, in strato 90–130 μ crassitudine sub cortice; medulla hyphis laxe intertextis crystallis saxi impleta. Apothecia 0.2–0.6 mm. diametro, orbiculata, disco ferrigineo-aurantiaco, amphithecio distincto, persistente, tenui, thallo concolore; epithecium crystallis brunneo-luteis inspersum; hypothecium hyalinum, centro circa 70 μ altitudine; thecium 63–87 μ altitudine; paraphyses filiformes, 1.7 μ diametro, simplices, septatae; asci 24–42 $\times$ 7–11 μ,

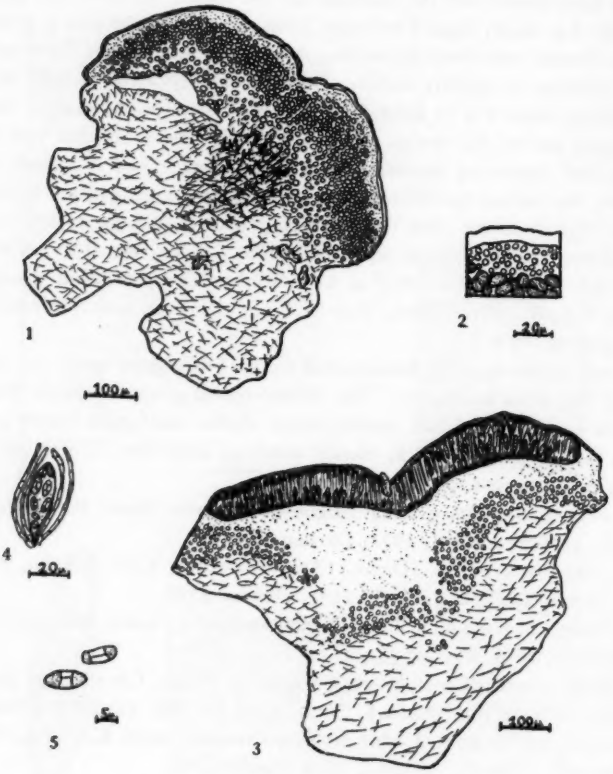

Fig. 2. *Caloplaca arizonica* E. Rud.

1. Section of thallus.
2. Enlarged section showing cortex.
3. Section of an apothecium.
4. Ascus with associated paraphyses.
5. Ascospores.

clavati; sporae 8-nae, 8.7–12.2 × 3.5–5.2 μ, polari-biloculares, isthmo circa 3 μ longitudine, uni- vel biseriales.

Thallus indeterminate, aerolate, fuscous, the areolae 0.5–1.0 mm., often quite far apart; cortex about 18 μ thick, with a gelatinous covering, fastigiate, KOH dark purple; algae protococcoid, forming a layer 90–130 μ thick below the cortex, the cells round to angular, 5–10 μ in diameter; medulla of loosely woven hyphae about 3 μ thick, containing numerous small rock crystals. Apothecia circular, 0.2–0.6 mm., disc brownish-orange, the margin persistent, thin, of the same color as the thallus; algae in the margin and in a layer below the hypothecium; epithecium incrusted with brownish-yellow crystals, about 13 μ thick; hypothecium hyaline, about 70 μ thick at center; thecium 63–87 μ high; paraphyses filiform, septate, about 1.7 μ thick, unbranched. Asci clavate, 24–42 × 7–11 μ; spores 8, uni- or biseriate, polar-bilocular, 8.7–12.2 × 3.5–5.2 μ, the isthmus about 3 μ long.

This species somewhat resembles *Caloplaca cinnabarina* (Ach.) Zahlbr., but can be distinguished by its relatively fewer and more dispersed apothecia, darker thallus, and narrower spores.

CALOPLACA CERINA (Ehrh.) T. Fries—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

CALOPLACA CINNABARINA (Ach.) Zahlbr.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on granite, 6500 ft., Dec. 24, 1933, *Darrow 471.*

CALOPLACA ELEGANS (Link) T. Fries—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16 & 20, Feb. 28, 1952, *Elmore.*

CALOPLACA FESTIVA (Ach.) Zwackh.—ARIZONA: Miller Canyon, Huachuca Mts., on igneous rock, 6300 ft., June 14, 1945, *Darrow 4243.*

CALOPLACA FULGENS (Swartz) Koerb.—ARIZONA: Nogales, on calcareous rock, 4000 ft., Oct. 6, 1946, *Darrow 4261;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

CALOPLACA LOBULATA (Floerke) Hellb.—ARIZONA: Pima Co., Rincon Mts., on granite, 4000 ft., March 4, 1934, *Darrow 785.*

CALOPLACA MODESTA (Zahlbr.) Fink—ARIZONA: Tucson Mts., on calcareous rock, 3000 ft., March 19, 1934, *Darrow 730;* Pima Co., Coyote Mts., on granite, 3200 ft., Feb. 16, 1945, *Darrow 4266.*

TELOSCHISTES PARIETINUS (L.) Norm.—NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Jan. 16, 1952, *Elmore.*

BUELLIA BLUMERI Zahlbr.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on igneous rock, 6500 ft., Dec. 24, 1933, *Darrow 477.*

BUELLIA RETROVERTENS Tuck.—ARIZONA: Whitehouse Canyon, Santa Rita Mts., on granite, 6500 ft., Dec. 24, 1933, *Darrow 489;* Tucson Mts., on volcanic rock, 3000 ft., March 19, 1934, *Darrow 736;* NEW MEXICO: Chaco Canyon, on sandstone, 6200 ft., Feb. 28, 1952, *Elmore.*

RINODINA **darrovii** E. Rud. sp. nov.—TYPE: ARIZONA: Santa Catalina Mts., on ground and moss, Nov. 12, 1933, *R. A. Darrow 498;* PARATYPE: Santa Catalina Mts., on soil, 8000 ft., Nov. 12, 1933, *Darrow 503.*

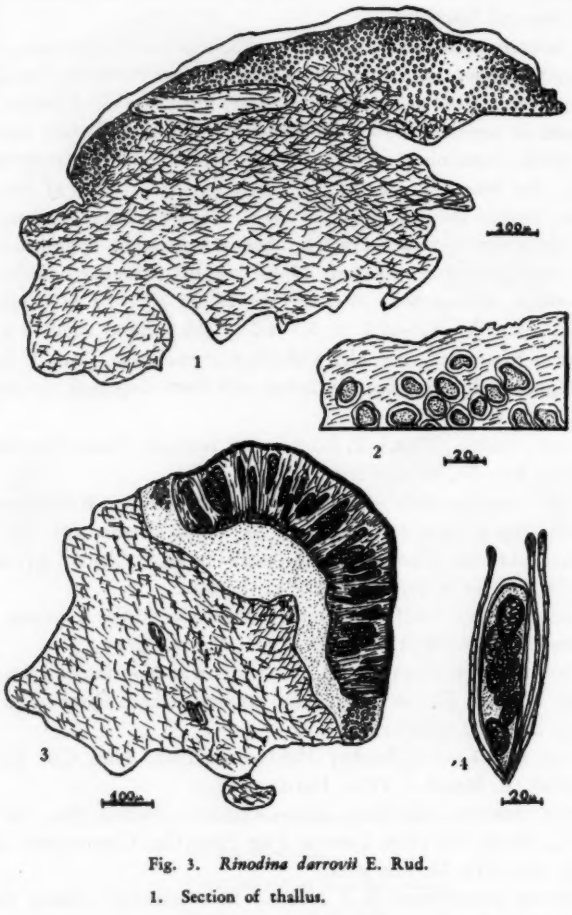

Fig. 3. *Rinodina darrovii* E. Rud.

1. Section of thallus.
2. Enlarged section showing cortex.
3. Section of an apothecium.
4. Ascus with associated paraphyses.

Thallus ochraceus vel cinnabarinus, granulosus, K—, diffractus; cortex gelifactus, erodus; algae protococcoideae, cellulis sphaericis vel angulosis, 5–10 μ diametro, in strato continuo 57–71 μ crassitudine sub cortice; medulla densa, hyphis indistinctis circa 1.5 μ diametro intertextis. Apothecia nigra, 0.5–1.0 mm. diametro, plana vel convexa; margine thalloideo, tenui, mox emarginato, thallo concolore; hypothecium hyalinum, in centro 80 μ altitudine; thecium 27–34 μ altitudine; paraphyses 2 μ diametro, septatae, simplices; asci 70–71 $\times$ 10–16 μ, clavati; sporae 8-nae, biseriatae, 17.4–24.4 $\times$ 8.7–11.5 μ, primo non-septatae, deinde tri-septatae, brunneae.

Thallus ochraceous-tawny to cinnamon-brown, granulose, broken in places into irregular pieces, KOH—; cortex gelatinous, eroded in parts; algae protococcoid, forming a continuous layer 57–71 μ thick, the cells spherical to angular, 5–10 μ in diameter; medulla of tightly woven, indistinct hyphae about 1.5 μ in diameter. Apothecia black, 0.5–1.0 mm. in diameter; disc flat to convex; margin thalloid, thin, of same color as the thallus, soon disappearing; hypothecium hyaline, of closely woven hyphae, about 80 μ thick at center; thecium 27–34 μ high; paraphyses filiform, septate, about 2 μ thick, swollen at tips and incrusted with yellow crystals, unbranched; asci clavate, 70–71 $\times$ 10–16 μ; spores 8, biseriate, brown, at first 1-celled becoming 4-celled, 17.4–24.4 $\times$ 8.7–11.5 μ.

This species has the general appearance of *Rinodina phaeocarpa* (Sommerf.) Vainio (*R. nimbosa* (E. Fr.) T. Fr.) but the four-celled spore places it in the subsection CONRADIA Malme as recognized by Zahlbruckner (1926). Its affinities seem to be with *R. conradi* Koerb. from which it can be separated by its larger black apothecia, its indistinct cortical hyphae, and its thicker hypothecium. The spores in this species have not been found to have more than four cells and also to be slightly smaller than those of *R. conradi*.

RINODINA EURYSPORA Zahlbr.—ARIZONA: Santa Rita Mts., on igneous rock, 7000 ft., Aug. 14, 1934, *Darrow 821*.

RINODINA NOVOMEXICANA B. de Lesd.—ARIZONA: Santa Rita Mts., on igneous rock, 4500 ft., June 3, 1934, *Darrow 707*; 7000 ft., Aug. 14, 1934, *Darrow 823*.

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THE ANALYSIS OF SUSPECTED HYBRIDS, AS ILLUSTRATED BY *BERBERIS* × *GLADWYNENSIS*

EDGAR ANDERSON

During the last fifteen years a considerable portion of my time has been spent in attempting to measure the importance of hybridization in the evolution of natural populations. More than a score of genera have been studied intensively in the wild (and whenever feasible in the breeding plot as well) with students and associates, though as yet only a fraction of these studies has been published. Various techniques have been worked out for dealing with such problems (Anderson, 1949, chap. 6), and as their validity has been more widely recognized (Stebbins, 1952) they are being more widely adopted. In the course of helping workers elsewhere to adapt these methods to their own problems I have become increasingly aware that in part they are based upon a scrutiny of the original material more exhaustive than is customary in many laboratories. It has accordingly seemed expedient to describe the procedure in more elementary detail than hitherto. Instead of discussing the complexities of hybridization in natural populations I have chosen the relatively simple example of an apparent hybrid which arose spontaneously in the garden of Mrs. J. Norman Henry, of Gladwyne, Pennsylvania. This seems a particularly happy choice since it also serves to demonstrate the usefulness of these methods in dealing with horticultural material of unknown ancestry.

A vigorous young barberry was found coming up in the shelter of a large bush of *Berberis verruculosa* in Mrs. Henry's garden. *Berberis verruculosa* is a dense, evergreen-leaved plant, certainly the most distinctive of the hardy barberries. The seedling, so obviously related that it must have been a seedling of *B. verruculosa*, was nevertheless so different from it that Mrs. Henry had supposed it was probably a spontaneous hybrid. It was different from any barberry known to her or to me and it exhibited the hybrid vigor which is the mark of so many hybrids. Furthermore, many garden hybrids of *Berberis* are known and Mrs. Henry at various times had grown a number of other species of *Berberis* in her garden. With her permission a precise examination was made both of the putative hybrid and of *Berberis verruculosa* to establish the probable ancestry.

The following is the procedure established in this laboratory for such examinations:

1. Choose comparable material of parent and hybrid.

2. Examine, describe, and measure each feature item by item. Use great care to work with truly comparable material. Do not attempt comparisons of a branch grown in the shade from one specimen and one grown in the sun from the other. If one is from a fruiting branch, then the other should be also. Use great care in distinguishing between long shoots and short shoots. Many plants without such conspicuously heterogeneous shoot systems as the *Ginkgo* have a more or less well-defined short shoot-long shoot system which requires careful examination to perceive.

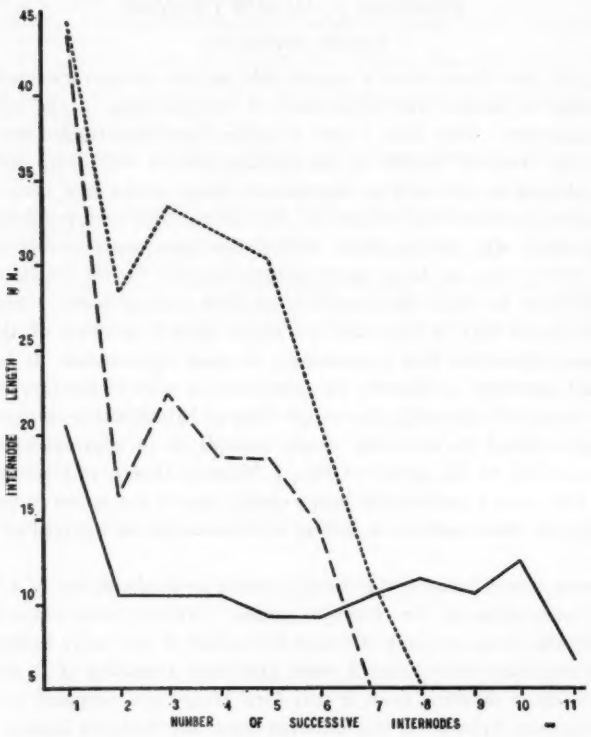

Fig. 1. Internode diagrams of comparable branchlets of two species of barberry and their putative hybrid. Solid line, *Berberis verruculosa;* long dashes, *Berberis* × *gladwynensis;* short dashes, *Berberis Julianae.* As explained in Anderson and Schregardus (1944), these diagrams are made by plotting the lengths of successive internodes from the base to the tip and connecting these points with an imaginary line. The first internode at the base of the branchlet in *B. Julianae,* for instance, is 45 mm. long, the second is 28 mm., the third, 33 mm., etc.

3. (And, most important): Conduct the entire examination, if possible, against a plain neutral background. Cover the table top with clean wrapping paper or some such material. Remove all distracting objects such as pencils, paper clips, erasers, etc., out of the immediate field of vision. The eye can work much more efficiently in the perception of resemblances and differences if it can concentrate upon the problem in hand. Work in a good light and have a good dissecting microscope. Choose a series of comparable branches and lay them out side by side with equal spacing. Choose a series of comparable leaves and lay them out side by side in the same manner, with their apices all pointing in the same direction. These seem like points much too elementary for serious scientific dis-

cussion, and yet in assisting other people to use my methods I nearly always find that these precautions have not been followed and that it is difficult to convince other scholars of their supreme importance. This is one of those ridiculously simple matters which are far more important than they seem and which are indicative of true scientific precision. Specific differences are frequently subtle and they can be apprehended much more readily if one uses comparable material, a neutral background, and a good light.

4. Make measurements with good steel calipers and a steel metric rule.

5. Pay particular attention to pubescence, pubescence pattern, internode pattern (Anderson and Schregardus, 1944), branching pattern. Careful analysis will show that nearly all closely related species of the higher plants differ significantly (and with enough study, definably) in their internode patterns.

Comparable branches were accordingly chosen from *Berberis verruculosa* and the seedling. Both were selected from well-developed branches of flowering age, growing in almost full sun and borne upon the upper parts of their respective plants. After these two branches had been examined carefully against a neutral background, comparable branchlets were chosen for further study as follows: Proceeding from the tip, the first strong secondary branch (all of the current season's growth) was selected for study. The internode lengths of this branchlet were measured to the nearest millimeter, the results being plotted as an internode diagram (fig. 1).

Hybrids are usually intermediate between their two parents when due allowances are made for heterosis, for growth-pattern differences, and for possible differences in ploidy. From a study of fig. 1, it is possible to make several predictions as to the putative male parent of the seedling barberry. *B. verruculosa* is shown to have more and shorter internodes than the seedling. Its basal internode is only about twice as long as the other internodes and the remaining internodes are subequal. The seedling has a basal internode more than twice as long as the others and the remaining internodes are not at all uniform in length and seem to have a definite pattern of decreasing length toward the tip. We therefore predict that the putative parent (when comparable material is studied) should have conspicuously non-uniform internode lengths with a very long internode at the base of such branches and decreasingly short ones as the tip is approached, probably in a well-defined pattern.

Leaf comparisons were then made. Choosing comparable leaves proved to be difficult but not impossible. Leaf size and shape were uniform in *B. verruculosa* but variable in the seedling. Care had to be taken, therefore, to choose exactly comparable material. Most of the primary leaves in these barberries are spines. The leafy leaves are borne on short secondary branches in the axils of the spine-leaves, giving the appearance of little clusters up and down the branches. In *B. verruculosa* all the leaves on the plant were superficially similar in size, shape, and serration. In the seedling they differed markedly. Those in clusters arising from the older wood were variable. Among them were leaves which were narrower

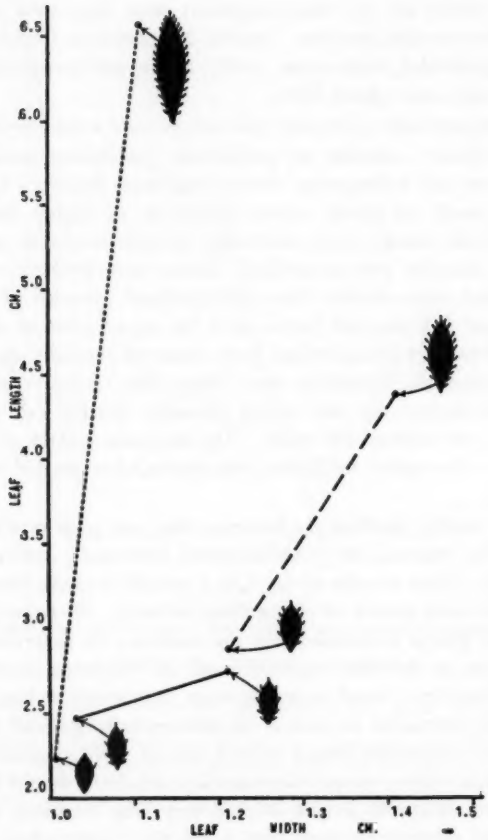

Fig. 2. Relationships of size, shape, and number of marginal setae in leaves from young and mature spurs for two species of barberry and their putative hybrid. As in the previous figure, a solid line indicates *B. verruculosa*, short dashes, *B. Julianae*, and long dashes, *Berberis* × *gladwynensis*, their putative hybrid. The figure shows simultaneously the length, width, and seta number of comparable leaves from young and from old spurs; the slope of the lines also indicates the change in shape from young to old: *Berberis Julianae* changes conspicuously in size, shape and seta number from young to old spurs; *B. verruculosa* scarcely at all; their hybrid is intermediate in degree of change. The silhouettes of leaf size and shape appended to the diagrams, while highly diagrammatic, are all to the same scale and represent average values from actual measurements.

in shape, larger in size and with more strongly developed setae at the tips of the serrations along their edges. Careful examination then showed that *B. verruculosa* had a very slight tendency in the same direction though not strong enough to be readily apparent without examination. Measurements showed that while *Berberis verruculosa* and the seedling had about the same number of setae per leaf on the new wood, the seedling had nearly twice as many as *verruculosa* on the old wood. Figure 2 shows all these relationships. The putative parent for which we are searching should have leaves on its new wood as small as those of *verruculosa*, or even smaller, with greatly differentiated leaves on the older wood. Some of the leaves on the older wood should be very long, proportionately narrow, and with many setae along their edges.

As, in this fashion, one proceeds feature by feature in the careful comparison of the one parent with the hybrid, he becomes progressively better acquainted with the general ground plan of the plant and is increasingly capable of making precise comparisons and valid inferences. Before long it is possible to draw up precise descriptions not only of *B. verruculosa* and its hybrid seedling but also of the putative male parent. Such a comparison is presented below in tabular form, including the predictions as to the male parent.

verruculosa	*gladwynensis*	unknown *(Julianae)*
Branches arching, sub-horizontal	Branches sub-arching, some nearly erect	Branches straight, erect to horizontal
Internodes short, uniform	Internodes medium, variable	Internodes long, very variable
Branchlets densely glandular	Branchlets at most sub-glandular	Branchlets eglandular
New growth scarcely differentiated	New growth clearly differentiated	New growth strongly differentiated
Mature bark barely ribbed	Mature bark definitely ribbed	Mature bark strongly ribbed and furrowed
Wood greenish	Wood yellowish-green	Wood bright yellow-green
Spines up to 1.2 cm.	Spines up to 1.3 cm.	Spines up to 1.5 cm.
Leaves glossy, dark green above, glaucous below	Leaves somewhat glossy, medium-dark above, sub-glaucous below	Leaves not glossy, bright green above, light green below
Fall color a more or less general purple	Fall color stronger on newest growth, occasional colored leaves	Brilliant fall color
Leaves on new and old growth scarcely differentiated	Leaves on new and old growth definitely differentiated	Leaves on new and old growth strongly differentiated
Largest leaves on old spurs 27 mm. × 12 mm.	Largest leaves on old spurs 43 mm. × 14 mm.	Largest leaves on old spurs 65 mm. × 11 mm.
10 marginal setae at most	20 marginal setae at most	Over 30 marginal setae
Flowers borne singly or in pairs	Flowers in fascicles of 5 to 8	Flowers in fascicles of 15 to 25
Stigma sessile	Stigma sub-sessile	Stigma definitely not sessile, style of at least 1 mm.

As the description began to resolve itself my knowledge of barberries was sufficient to suggest that *Berberis Julianae* was probably the barberry we were looking for. As soon as I made this suggestion Mrs. Henry informed me that a large bush of this species had once stood just a few feet away from *B. verruculosa* but it had been damaged in a windstorm and removed. Many of the technical points in the description, however, involved matters which were completely outside my knowledge of barberries. Predictions as to the numbers of setae on the mature leaves, the number of flowers per fascicle, the presence of a style, etc., were drawn up with no knowledge of what they might be like in *B. Julianae*. The entire hypothetical description was then run down in Rehder's key (Rehder, 1940) to the barberries just as if one had the specimen actually in his hand. It led to *B. Julianae* and fitted the description of that species precisely, down to the most technical detail.

There can be little doubt, therefore, that the seedling was a spontaneous hybrid, *B. verruculosa* × *B. Julianae*. I am accordingly describing it as:

Berberis × **gladwynensis** hyb. nov.[1] Intermediate between its parents *B. verruculosa* and *B. Julianae*. Flowers in fascicles of 5 to 8, stigma subsessile, leaves subglaucous below, nearly evergreen. Type: *Henry*, in the herbarium of the Philadelphia Academy of Natural Sciences; from the type bush, *E. Anderson s. n.*, MBG.

It is a pleasure to name this handsome barberry after the site of Mrs. Henry's garden which has long been a mecca to botanists and gardeners alike.

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[1] Berberis **gladwynensis** hyb. nov. inter parentes *B. verruculosam* et *B. Julianam*. Flores in fasciculis 5–8, stigmate subsessile. Folia fere semperviridia, subter subglauca.

VARIATION IN COB MORPHOLOGY AMONG CERTAIN ARCHAEOLOGICAL AND ETHNOLOGICAL RACES OF MAIZE

NORTON H. NICKERSON*

Introduction

Zea Mays L., one of the most highly evolved of all grasses, is still botanically much of an enigma. Commonly known as Indian corn or maize, it was a very important plant to the peoples of the New World long before the arrival of Columbus. It formed the basis of the highly developed Inca, Maya, and Aztec civilizations and was the staple crop from Canada to Chile for several thousand years. It is, of course, quite important to the present-day inhabitants of Central and South America, and agriculture and industry in the United States uses three and one-quarter billion bushels annually.

Botanists have until recently followed almost exclusively Sturtevant's (1899) classification of contemporary races of maize by kernel types. Although this classification is an artificial one, it has proven to be of practical commercial worth. Archaeologists have long known the value of maize kernels found at excavation sites for determining types of maize grown and the uses to which they were put. Until the last few years, other parts of the maize plant have been quite generally neglected as a source of historical data, chiefly because of the complexities involved in determining and evaluating such evidence as they contain. Evidence from maize tassels has been used with promising results (Alava, 1952; Anderson, 1944b, 1944c, 1949a, 1951; Anderson and Brown, 1948; Anderson and Cutler, 1942; Brown *et al*, 1952; Cutler, 1946; Wellhausen *et al*, 1951, 1952). Prat (1948) showed that in maize and other grasses hairs and other epidermal emergences can be used as a basis for identification and classification. Internode patterns have been studied by several workers (Anderson, 1943, 1949a; Anderson and Brown, 1948; Anderson and Schregardus, 1944; Stonor and Anderson, 1949; Wellhausen *et al*, 1951, 1952). Ear and tassel ontogeny have been studied by Bonnett (1940, 1948) and Kiesselbach (1949). Esau studied the ontogeny of the maize vascular bundle.

Surprisingly little has been done to measure and evaluate those morphological structures which are present on a maize cob after the kernels have been removed. Weatherwax, a pioneer in the study of the maize cob, pointed out (1918) the need and value of accurate morphology in understanding this structure, and demonstrated (1920) the orderly spikelet behavior underlying changes in kernel rowing. Fujita (1939) observed that an even number of pairs of kernels resulted in straight rows, and an odd number in spiral rows. Cutler (unpublished work) made many histological studies of the cobs of both North and South American maize, as well as of several closely related genera. Lenz (1948) indicated the types

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The stimulating advice of Dr. Edgar Anderson and the technical assistance of Mr. Ding Hou throughout the course of this investigation are hereby gratefully acknowledged.

of evidence available from a histological study of the maize cob. Alava (unpublished work) modeled in great detail small portions of the exterior surface of a maize cob. Mangelsdorf and Smith (1949) tabulated a number of external and internal maize ear characters, and their general procedure was used in characterizing 25 present-day races of maize in Mexico by Wellhausen *et al* (1951, 1952). These studies were based on the evaluation of many characters which did not involve exact measurements. In the present study, the value of several morphological characters used by these investigators has been increased by employing exact measurements. Other measureable morphological characters have been found which are of significance in tracing historical influences of one race of maize upon another.

There are two reasons why evidence present on the maize cob is important. The first one is based on the generally accepted fact that distinguishing characters are not distributed at random among plants; with regard to their occurrence in the Maydeae, agrostologists have found the female inflorescence to be of particular significance. The second reason, already pointed out by Lenz (1948), is that there are more archaeological remains of maize cobs than of any other plant material. The importance of these remains can perhaps be appreciated when one considers that maize, unlike most cultivated crops, is completely dependent upon man for its preservation. This fact can only mean that it has had a constant association with man since its adoption as a food plant, and that in its manner of origin, in the course of its migrations, in its development into a myriad of races, and in its intimate association with ancient religious symbolism, the history of maize becomes intimately tied to the history of man. Increased insight into the one will certainly add to our present understanding of the other.

For a reasonably complete investigation of the maize cob, the following three courses were deemed necessary: (1) to measure certain easily-recognized features of the maize cob and to interpret their morphological nature; (2) to set forth one possible scheme of analysis of the variation patterns of different races of maize based on these measurements; (3) to discuss the resulting indicated trends as to their validity and applicability in extending our present understanding of the history of maize.

Morphology of the Ear

Bearing in mind that an adequate treatment of variation in maize ears would be more complete if the nature of those parts under discussion were understood, a detailed study of morphological structures found on the maize ear was first undertaken. However, since the results are of a technical nature quite different from those obtained from a study of variation, they are treated elsewhere (Nickerson, in press).

MORPHOLOGICAL STRUCTURES EXAMINED

One of the purposes of this study in variation is to determine what morphological structures expressed in the cob are of significance in differentiating between races of maize. To accomplish this, several characters had to be included which ultimately proved to be of little use. A total of 526 cobs was examined for each of the three external and five internal characters discussed below.

EXTERNAL CHARACTERS

Shape of Ear.—This character is the only one used in the investigations which is dependent upon a subjective grading. Ears were classified into one of four types: straight, cigar-shaped, tapered, enlarged butt. Two of these types—straight and tapered—were used in analysis of each sample. For reasons discussed elsewhere (Nickerson, in press), a straight-eared race exhibits less condensation than a tapered- or enlarged butt-eared race, and a race with cigar-shaped ears is intermediate between these extremes.

Shank Diameter.—The diameter of the shank was measured in millimeters at a point close to the base of the ear, above the last apparent husk node whenever possible. In specimens with elliptical shanks, two measurements were made and an average of these was used. Shank diameters are fairly consistent within any one kind of maize and are often markedly divergent between different kinds.

Row Number.—Row number was determined by counting the number of vertical rows of glumes in the middle area of the cob. The middle area was used for this and all subsequent measurements because of its uniformity of size, stage of development, and freedom from growth irregularities common at both base and tip of the ear. Row number is a readily-observed character the importance of which is not yet fully understood. Anderson and Brown (1948) were able to correlate the condensation index of the tassel with kernel row number in the ear. Cutler (1952) used row number in his preliminary study of cobs from successive layers of cultural remains found in Tularosa Cave. His tables indicated the presence of high row numbers in lower strata and progressively lower row numbers in successively higher strata. These data show the reverse of the situation reported for the stratified remains of Bat Cave by Mangelsdorf and Smith (1949), who stated that in general the older (and more pod-corn-like) the ear, the lower was its row number.

INTERNAL CHARACTERS

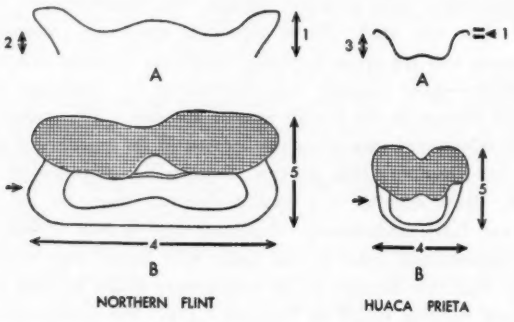
To study internal characters, the ear was broken in two at the approximate middle; the exposed ends were then observed under a dissecting microscope.

Width of Lower Glume.—This character was measured in millimeters with the calipers held perpendicular to the widest point on the abaxial surface of the glume. The measurement is not a direct expression of a particular gene such as Mangelsdorf and Smith (1949) reported for the relationship between lower glume length and various alleles of the *Tu* gene, but reflects the width of the basal portion of the kernel which it encloses.

Height of Rachis-flaps.—This measurement in millimeters was made perpendicular to the axis of the cob. In instances where the rachis-flaps were of unequal height, an average measurement was used. The rachis-flap is a part of the cupule (Nickerson, in press) and its significance is somewhat minimized by its variability in some otherwse homogeneous samples used in the present investigation. Mangelsdorf and Smith (1949) reported the same situation for maize cobs from Bat Cave, but Wellhausen *et al* (1951, 1952) found rachis-flaps to be extremely useful in characterizing races of maize in Mexico.

Depth of Cupule.—This measurement in millimeters was made perpendicular to the cob axis, and was given a positive or a negative value, depending upon whether it was out from, or down into the rachis. It represents the extent of adnation of the cupule-forming prophyll (Nickerson, in press) to the axis, and is well correlated with ear shape.

Width of Cupule.—This measurement was made by holding the calipers at right angles to the cob surface and measuring the distance in millimeters between



Text-fig. 1. Drawings of two representative maize races showing distances measured in determining four internal cob characters. A, transverse section of cupule; B, external view of cupule after glumes and spikelet pedicels have been removed. Shaded areas represent points of attachment of spikelets and glumes. Arrow at left of B indicates the point at which a transverse cut was made in each case to obtain the view shown in A. Drawings are to scale; arrows at 2 and 3 are each 1 mm. long.

any pair of outside rachis-flap edges across their cupule. It is in part an indication of kernel width, in that wide cupules always mean wide kernels.

Thickness of Kernel.—The distance along the cob axis from the base of one set of lower glumes to the upper edge of their cupule is exactly equivalent to the thickness of each kernel produced there. The measurement is useful in making comparisons between productivity of different cob samples, especially those involving fragmentary archaeological remains.

These last four characters were recorded in outline drawings carefully made to scale (working with calipers under a dissecting microscope) for each of the 526 cobs examined (text-fig. 1). Other characters measured but not used include height and texture of the lower glume and longitudinal profile drawings of each cupule. Diameters of the pith, cob, and rachis were measured and the cob/rachis index (Mangelsdorf and Smith, 1949), as well as the rachis/pith index, was computed for all specimens. However, neither the averages nor the individual variations of these indices were found to be particularly characteristic among the maize samples studied in this investigation.

Names, Sources, and Anthropological Background of Samples

Maize samples examined were of diverse origin both geographically and temporally. Races of contemporary maize here included were chosen as typical for those parts of the world. Archaeological cob samples were largely from the southwestern United States, but included one sample from Lower California and two extensive collections from sites excavated by Junius Bird in Peru and northern Chile. In listing the samples they are grouped arbitrarily into geographical units; no further inferences should be drawn from this arrangement. Samples, except where otherwise noted, are from the maize collection of the Museum of Economic Botany of the Missouri Botanical Garden, St. Louis.

NORTH AMERICA

Present-day Races:

Iroquois Sacred Flour.—This sample was from material originally grown by Professor Frank P. Bussell from seed collected by Erl Bates from the Iroquois Indian tribes of northern New York. The Indians grew it under conditions of strict isolation for ceremonial use (Anderson, 1947b). Ears are straight, 20–28 cm. long, with heavy shanks and 8 rows of wide white or yellow (sometimes pale blue) kernels. Fourteen ears were examined.

Northern Flint.—A composite sample, this group included flint corns from the Northeast (Parker's, Canada, Mammoth Yellow, Longfellow) and the upper Great Plains (Winnebago, Bear Island, Brownell, Mandan, Tama, Golden Chippewa). Brown and Anderson (1947) studied these and other representative flint varieties and reported that the ears were long and slender with 8–10 rows of wide, crescent-shaped kernels, heavy shanks, and a tendency toward a large cob base. Twenty-three ears were examined.

Hopi White Flour.—This sample was furnished by Dr. William L. Brown, Pioneer Hi-Bred Corn Co., Johnston, Iowa, who collected it at the Hopi town of Hotevilla, Arizona. Carter and Anderson (1945) considered Hopi White Flour to be an example of Puebloan maize. Brown *et al* (1952) reported that this variety is one of their main sources of meal. The straight ears are 18–24 cm. long, with wide shanks, no basal compression, and wide white kernels in 12–14 rows. Seven ears were examined.

Hopi Blue Flour.—Also furnished by Dr. William L. Brown, this collection has substantially the same history as Hopi White Flour. However, Brown *et al* (1952) reported that it is probably more important as a source of food. The cigar-shaped ears are 14–20 cm. long, with small shanks, a tendency toward basal compression, and 10–20 rows of narrow blue-aleuroned kernels with white endosperm. Eleven ears were examined.

Papago Flour.—This race of maize is grown by the desert-dwelling Papago Indians, and was reported by Carter and Anderson (1945) to be quite similar to prehistoric Basketmaker maize. The ground kernels make a meal of excellent quality. Ears are 20–25 cm. long, cigar-shaped, with narrow shanks and 12–14 rows of isodiametric yellow kernels with white endosperm. Twenty-five ears were examined.

ARCHAEOLOGICAL REMAINS:

Basketmaker.—Cobs included in this collection were recovered from Kinboko and White Dog Caves, both of which are located in Tsegi Canyon, Marsh Pass, northeastern Arizona. The samples were submitted by Mr. Harold S. Gladwin, who estimated their age to be *circa* 200–300 A.D. On the basis of there being no pottery associated with these cobs, they are believed to belong to the cultural level known as Basketmaker II. The cigar-shaped cobs are 6–12 cm. long, and bore somewhat isodiametric kernels in an average row number of 14. Six cobs were examined.

Marsh Pass.—Cobs included in this collection were recovered in West Hackberry Canyon and Turkey Cave, both of which are located in Tsegi Canyon, Marsh Pass, northeastern Arizona. These samples were also submitted by Mr. H. S. Gladwin, who estimated their age to be from 300 A.D. to about 1000 A.D. The collection represents cultural levels from late Basketmaker II or later up through Pueblo II. The predominantly cigar-shaped cobs are 6–14 cm. long, and bore kernels wider than thick in an average row number of 10. Thirty-one cobs were examined.

Turner Site.—This sample consisted of 50 cobs and fragments recovered from the Turner Site, near Cisco, Utah, by H. M. Wormington, Curator of Archaeology, Denver Museum of Natural History. Wormington estimates its age to be around 1000 A.D. (personal communication, 1953), and believes that the site was inhabited by peoples who were culturally a later manifestation of the Fremont Basketmakers. Remains of their culture were recovered from Castle Park in the

Yampa River Valley, Utah, and are dated at 400–800 A.D. by Burgh and Scoggin (1948). There are nearly equal numbers of tapered and cigar-shaped cobs in this collection; some were not used in this study because of their fragmentary nature. Cobs are short, 3–8 cm. long, charred, with medium shank diameters and medium-wide kernels in an average number of 12 rows. Twenty-seven cobs were examined.

Luster Cave.—Ten cobs were recovered by Dr. Robert Lister, Department of Anthropology, University of Colorado, Boulder, from a cave located in Utah, just west of the Colorado state line, in the Glade Park area. A preliminary report (Lister and Dick, 1952) described the archaeological finds of this cave and of other nearby sites. On the basis of pottery types, the maximum possible age assigned to Luster Cave by these workers is 900–1000 A.D., but it may be much more recent. The straight and tapered cobs are generally uncharred and fairly complete with small shank diameters and wide kernels in an average number of 10 rows. Nine cobs were examined.

Tularosa Cave.—More than 30,000 maize cobs were recovered from this site in Pine Lawn Valley, northeast New Mexico, by archaeologists from the Chicago Natural History Museum. The Museum has submitted these cobs to Dr. Hugh C. Cutler, who has generously made available for inclusion in the present study samples representing three levels of Square 3R2. Maize cobs from the lowest levels of Tularosa Cave were dated at 2300 ± 200 years by the Carbon 14 method. The cave is estimated to have been abandoned somewhere around 1000–1200 A.D., and thus was continuously occupied for about 1500 ± 500 years (Martin *et al*, 1952). Material from Square 3R2, Levels 3, 6, and 11 was studied as three separate samples, each of which was chosen so that the cobs analyzed reflected the proportionate row numbers determined by Cutler (1952) from all cobs found in each of these layers. There was a decrease in row number from the lower levels to the surface, average row numbers for Level 11 being 12–14, for Level 6, 10–12, and for Level 3, 8–10. Culturally, Level 11 is the oldest (400 B.C. ± 200 years) and represents the Pre-pottery Phase. Level 6 dates back to 500–600 A.D., and represents the Georgetown Phase. Level 3, at 1000–1200 A.D., represents the San Francisco Phase. Twenty-five cobs from each of the three levels were examined.

Point of Pines.—This sample consists of about 250 ears of charred maize. It was recovered from Room 50 of a large ruin at Point of Pines, Arizona, numbered Ariz. W:10:50, and was submitted by Dr. Emil W. Haury, Director, Arizona State Museum, Tucson, Arizona. He believes its age to be 1250 A.D. (personal communication, 1953). It can be assigned to the Pueblo II cultural phase. The straight and cigar-shaped ears are 5–8 cm. in length, with small shanks and smooth kernels wider than thick in an average number of 10 rows. Seventy-five cobs were examined.

MEXICO AND CENTRAL AMERICA

PRESENT-DAY RACES:

Chapalote.—This race of popcorn is considered by Wellhausen *et al* (1951, 1952) to be one of the ancient indigenous races of Mexico. It was mentioned by Anderson (1944a, 1946) as being allied to the primitive *Maíz reventador.* Wellhausen *et al* pointed out its resemblance to archaeological maize finds at Painted Cave (Haury, 1945) and Cottonwood Cave (Hurst, 1948; Hurst and Anderson, 1949). They considered it to be one of the most distinctive races of maize in Mexico. Mangelsdorf (1948) and Mangelsdorf and Smith (1949) regarded it as possessing the "weak" allele for pod corn. The cigar-shaped ears are 10–15 cm. long, with small shanks and smooth rounded chocolate-brown kernels in an average row number of 12. Ten ears were examined.

Guatemala Flint.—A common variety of the Guatemala highlands, this race was described by Anderson (1947a), who considered it to represent one of the basic elements in Guatemalan maize. Ears are 10–25 cm. long, with a conspicuously enlarged and irregularly rowed butt, heavy shanks, a heavily sclerenchymatized rachis, and wide flinty kernels (some of which are capped with soft starch) in 8 (occasionally 10 or 12) straight rows. Eleven ears were examined.

ARCHAEOLOGICAL REMAINS:

Lower California.—This sample of 52 maize remains was recovered from Cave B. C. 100, located 8–10 miles east-southeast of Comondu, in central Baja California, and was submitted by Dr. William C. Massey, Dept. of Anthropology, University of Washington, Seattle. The cobs were recovered from a layer dated by Dr. Massey at 1697–1750 A.D. (personal communication, 1953). The cigar-shaped and straight cobs are 6–12 cm. long, with small shanks, and bore nearly isodiametric kernels set in 10–12 rows. Thirty-five cobs were examined.

SOUTH AMERICA

PRESENT-DAY RACES:

Peru Flour.—This sample was collected by G. Edward Nicholson at Huancayo, Peru, where it was being offered for sale in one of the native markets under the name of *"Maíz de Color."* It belongs to the race Cutler (1946) called "Valle Maize." Ears are short, tapering, constricted at the base, with small shanks. The race exhibits little sclerenchymatization. Kernel color varies from ear to ear; brown, red, yellow, and various delicate striped combinations are most common. Kernels are pointed, as wide as thick, and arranged in prominent rows averaging 10 per ear. Twenty-three ears were examined.

Coroico.—This race, described by Cutler (1946) as "the most unusual race so far known," has the odd characteristic of brick-like arrangement of "alicoles" (cupule plus pair of associated spikelets; Nickerson, in press). Cutler described the tapered ears as long, slender, and flexible (25–30 cm. lengths were common in the collection examined), with a light brown cob, small pith, and brown-orange

kernels. He stated that the row number averaged 9, but he now believes (personal interview, 1953) that two successive rings of alicoles constitute a single diametral whorl; thus the row number of Coroico is generally high, averaging 18. Whether 9 or 18 rows are present is governed by the state of condensation of the cob axis. Twenty-five ears were examined.

ARCHAEOLOGICAL REMAINS:

Arica.—These samples were recovered from two midden sites, Playa Miller and Quiani, located on the coast in the vicinity of Arica, Chile (18° 30′ S. Latitude), by Junius B. Bird, Associate Curator of Archaeology, American Museum of Natural History, New York. Cobs from both sites were treated as one sample following Bird's (1943, 1948) suggestion that Playa Miller represented a continuation of sequences started at Quiani. The oldest maize remains from this area are dated at about the time of Christ (Bird, personal communication, 1952). It is thus younger than material from the Huaca Prieta sites discussed below. The cigar-shaped and tapering cobs are 5–12 cm. in length and 1–2.5 cm. in width, with small shanks and an average row number of 14. Twenty-one cobs were examined.

Huaca Prieta.—These samples, also from the American Museum, were recovered by Junius B. Bird from Huaca Prieta, a site on the Peruvian coast at the south of the Chicama Valley (app. 8° S. Latitude). These comprehensive samples consist of 604 cobs from Test 1 and 171 cobs from Test 5. The two groups were treated separately, since Bird regarded cobs from Test 5 as older than those from Test 1, and were designated Huaca Prieta 5 and Huaca Prieta 1, respectively. Cultures responsible for the Huaca Prieta middens began about 3000 B.C. (Bennett, 1948; Bird, 1948), but maize did not make its appearance there until 850 B.C. (Bird, personal communication, 1953). Implications as to archaeological and botanical significance of these finds are further discussed by Anderson (1947b), Carter (1950), and Whitaker and Bird (1949). The well-preserved, tapered and cigar-shaped cobs are remarkably uniform, especially those found in the lower levels, which have small shank diameters, an average row number of 14, and are horny rather than brittle or bony in texture. Thirty-five cobs from Huaca Prieta 1, representing 7 layers, and 44 cobs from Huaca Prieta 5, representing 5 layers, were examined.

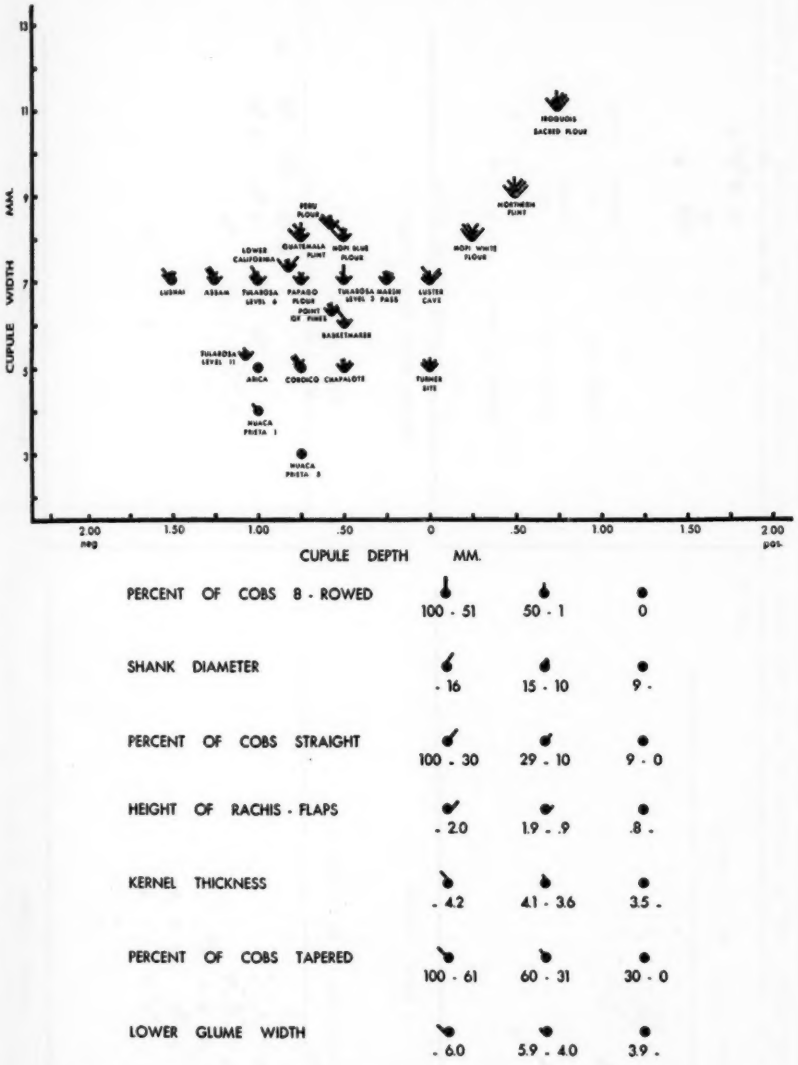
ASIA

Assam and Lushai.—The samples from Asia were contributed by Stonor, who collected them in the hills of Assam. The history and morphology of varieties in this collection have been described by Stonor and Anderson (1949). The cobs used here were those actually raised in Asia. For this investigation they were separated into two groups: (1) *Assam,* which includes 21 cobs from tribes other than the Lushai; (2) *Lushai,* which includes 8 cobs representative of the maize varieties grown by the Lushai tribe. Cobs of both groups are sufficiently alike to

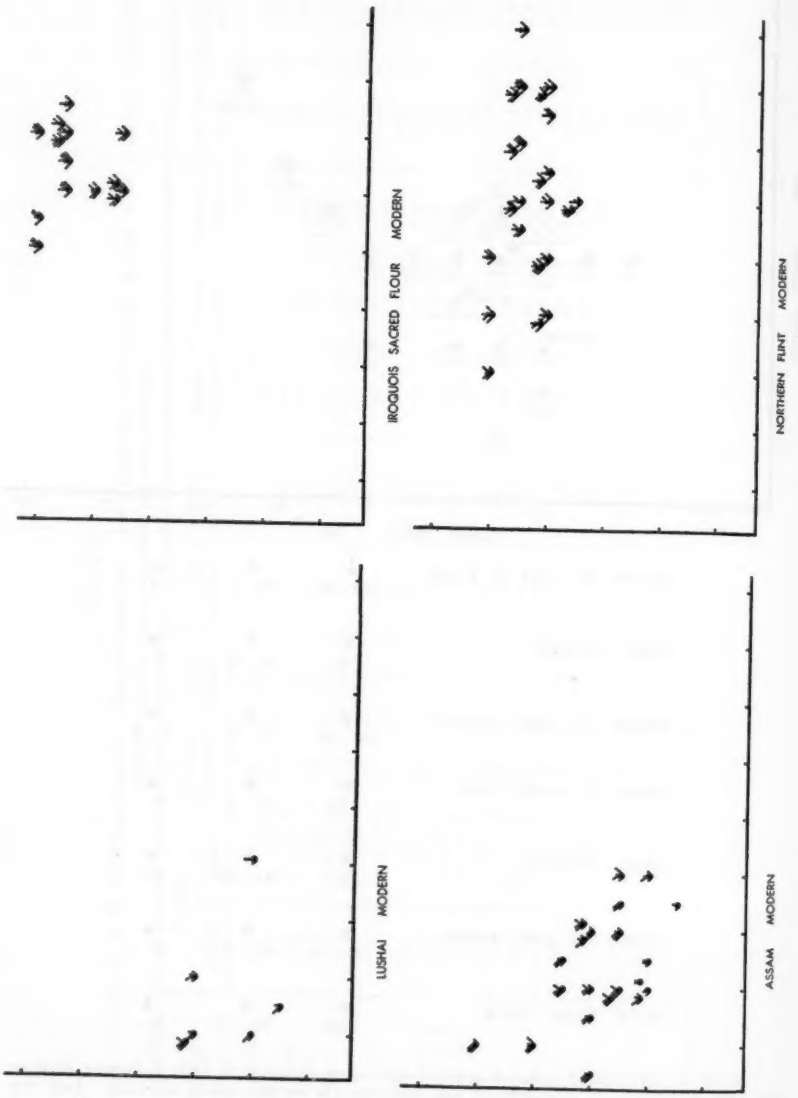
TABLE I

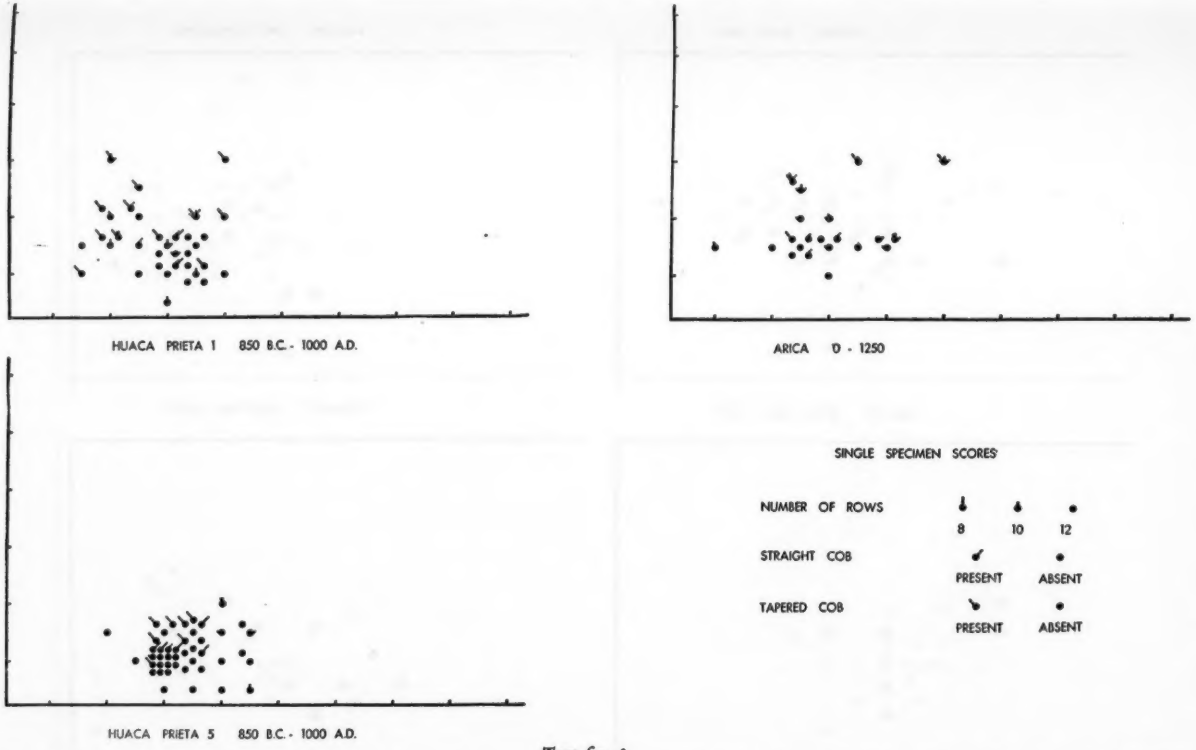
AVERAGE VALUES OF NINE MORPHOLOGICAL CHARACTERS AND TWO INDICES FOR EACH MAIZE COB SAMPLE STUDIED
(Measurements in mm. except where otherwise indicated)

Name of Sample	Cupule		% cobs 8-rowed	Shank diameter	% cobs straight	Height of rachis flaps	Kernel thickness	% cobs tapered	Lower gl. width	Cob/rachis index	Rachis/pith index
	width	depth									
Iroquois Sacred Flour	11.5	+ .75	90	22	43	2.0	3.7	43	8.7	1.7	2.1
Northern Flint	9.5	+ .50	90	16	35	2.0	4.4	32	7.0	1.8	2.1
Hopi White Flour	8.5	+ .25	0	19	35	2.0	4.7	65	6.2	1.7	1.8
Hopi Blue Flour	8.5	— .50	20	12	35	1.6	4.2	0	5.8	1.9	1.8
Papago Flour	7.0	— .75	0	14	0	1.2	4.0	28	5.4	1.8	1.9
Basketmaker	6.0	— .50	0	9	0	1.5	4.3	16	4.4	1.6	2.0
Marsh Pass	7.5	— .25	20	11	16	1.5	4.1	20	5.5	1.5	2.1
Turner Site	5.5	0	11	8	12	1.0	3.0	50	3.7	1.3	1.7
Luster Cave	7.5	0	33	7	33	1.6	4.5	33	5.2	1.8	1.8
Tularosa Cave—L. 3	7.0	— .50	68	9	0	1.5	4.1	4	5.9	1.8	2.4
Tularosa Cave—L. 6	7.5	—1.00	16	7	4	1.3	4.7	48	5.5	1.7	2.3
Tularosa Cave—L. 11	5.5	—1.00	0	8	0	1.0	4.0	4	5.5	1.7	2.3
Point of Pines	6.5	— .50	32	8	20	1.2	3.6	3	5.5	1.7	2.0
Chapalote	5.5	— .50	10	9	0	1.0	4.0	10	5.4	2.1	2.5
Guatemala Flint	8.5	— .75	77	15	0	1.2	4.5	44	6.8	1.9	2.9
Lower California	8.5	— .75	14	8	37	1.3	3.8	27	5.9	1.8	2.1
Peru Flour	8.0	— .50	10	8	8	.9	4.0	92	5.0	1.9	2.2
Coroico	5.5	— .75	0	13	0	.5	6.6	95	5.9	1.9	2.1
Arica	5.0	—1.00	0	6	0	.5	3.2	30	3.5	1.6	2.1
Huaca Prieta 1	4.0	—1.00	0	4	5	.3	3.1	31	2.4	1.6	1.8
Huaca Prieta 5	3.5	— .75	0	6	9	.2	3.0	13	2.7	1.9	1.9
Assam	7.0	—1.25	0	12	0	.9	4.9	75	5.0	1.7	2.3
Lushai	7.0	—1.50	12	10	0	.5	4.0	75	6.0	1.9	2.0



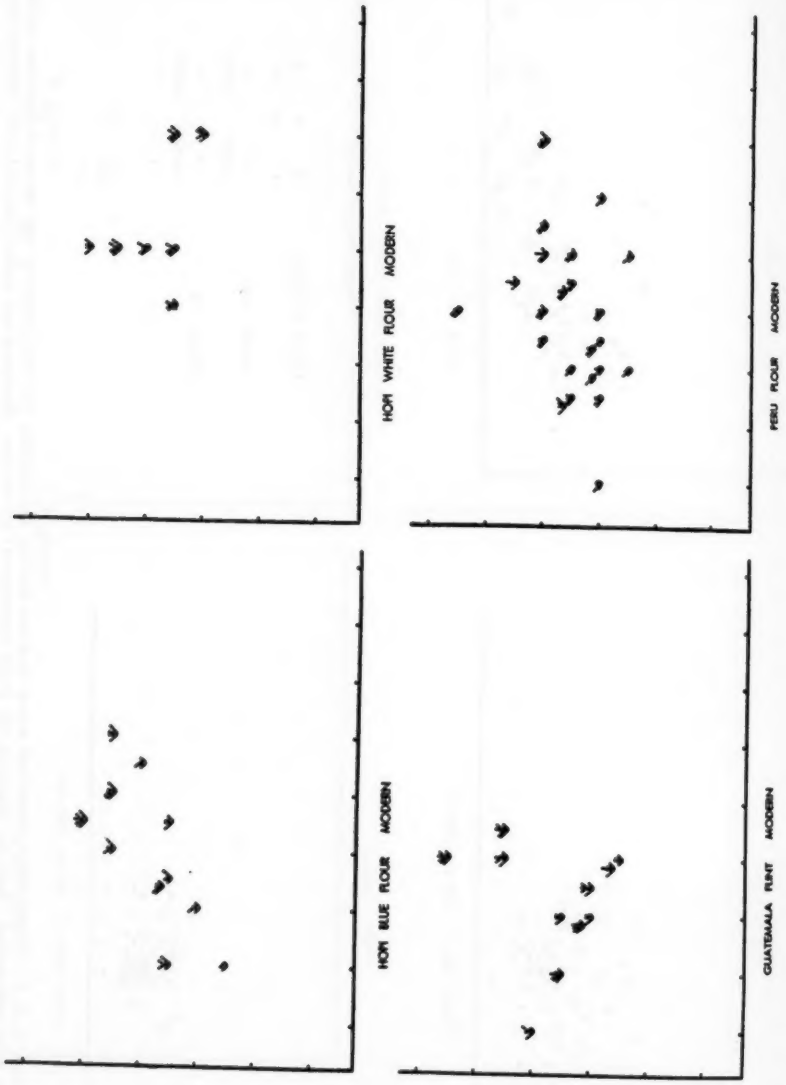
Text-fig. 2. Pictorialized scatter diagram of information contained in Table I, showing relationships between variation in nine different cob characters for various samples of maize. Each dot represents the mean for nine measured characters for all cobs studied in that group; horizontal axis, depth of cupule; vertical axis, width of cupule; seven other characters are diagrammed by rays, as explained on the figure. Further explanation in the text.

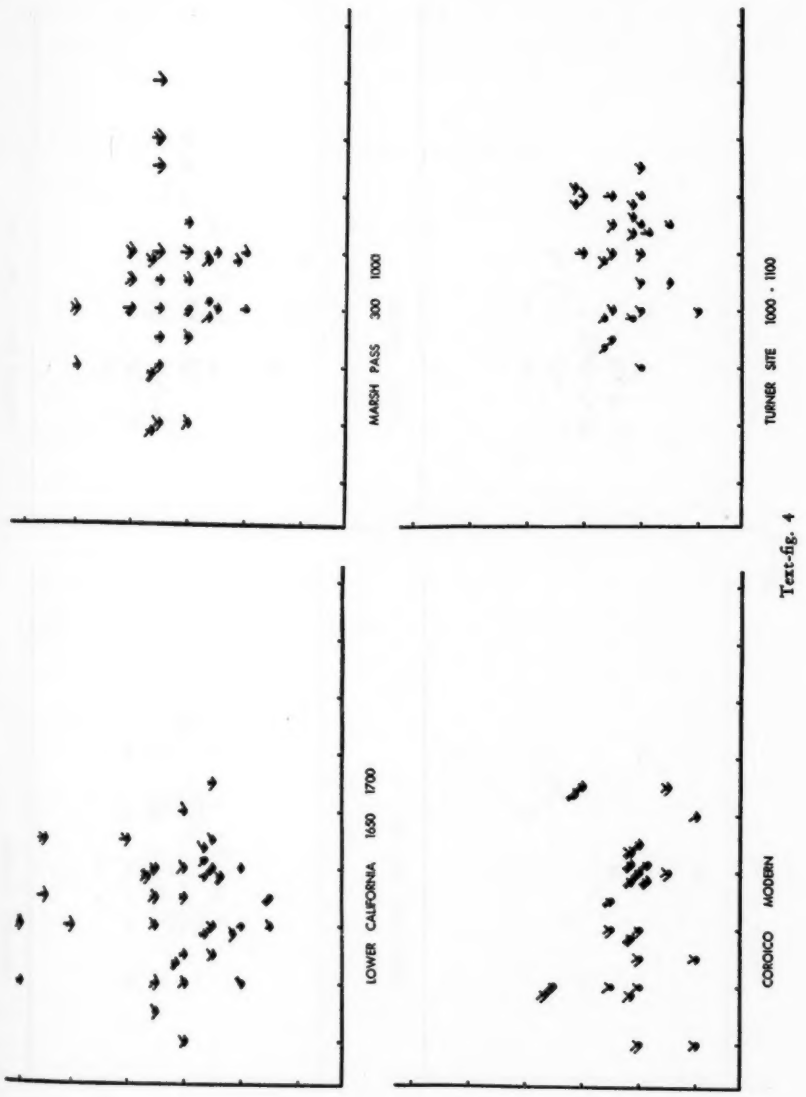

IROQUOIS SACRED FLOUR MODERN
NORTHERN FLINT MODERN
LUSHAI MODERN
ASSAM MODERN



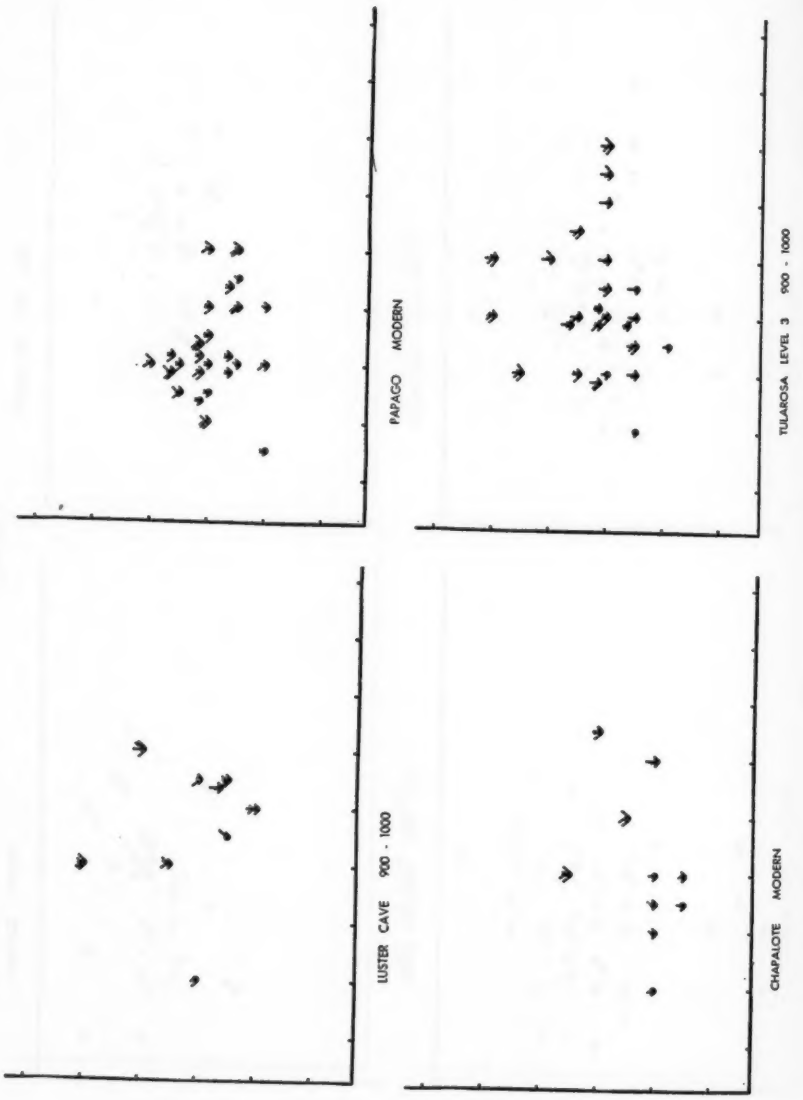
Text-fig. 3

Text-figs. 3, 4, 5. Twenty-three pictorialized scatter diagrams showing the variation and relationships of nine measured characters within each group of maize cobs studied. Each dot represents the actual measurements for one ear. Horizontal and vertical axes and seven additional characters are scored as in text-fig. 2, except row number and cob shape, which were scored as indicated in the lower right-hand corner of text-fig. 3. Dotted ray indicates no measurement could be made.


HOPI WHITE FLOUR MODERN
PERU FLOUR MODERN
HOPI BLUE FLOUR MODERN
GUATEMALA FLINT MODERN


MARSH PASS 300 1000
TURNER SITE 1000 - 1100
LOWER CALIFORNIA 1650 1700
COROICO MODERN

Text-fig. 4


PAPAGO MODERN
TULAROSA LEVEL 3 900 - 1000
LUSTER CAVE 900 - 1000
CHAPALOTE MODERN

TULAROSA LEVEL 6 500 - 700
TULAROSA LEVEL 11 300 B.C. - 150 B.C.
POINT OF PINES 1250 1300
BASKETMAKER 200 300

Text-fig. 5

conform to the same general description. They are tapered, 15–25 cm. in length, with a medium-sized shank and bore 14–16 rows of narrow kernels. That they are markedly lighter in weight than ears of North and Central American maize of comparable size is undoubtedly another expression of their lack of heavily sclerenchymatized tissues.

Measurements of Samples

The number of cobs in each of the above-listed samples varied, but an attempt has been made to examine enough cobs to form consistent pictures of variation in the populations represented. Measurements recorded for each cob include, in addition to those of four external and five internal characters mentioned earlier, diameters of cob, rachis, and pith. From these last measurements, a cob/rachis index and a rachis/pith index were computed.

Since plants are affected by their environment in numerous ways, several representatives of any population must be studied to formulate a complete picture of their range of variation. This idea applies quite as much to archaeological remains as to living plants, for, as Cutler (1952) has pointed out, a single specimen of any archaeological plant remains is of little significance; it may represent

TABLE II

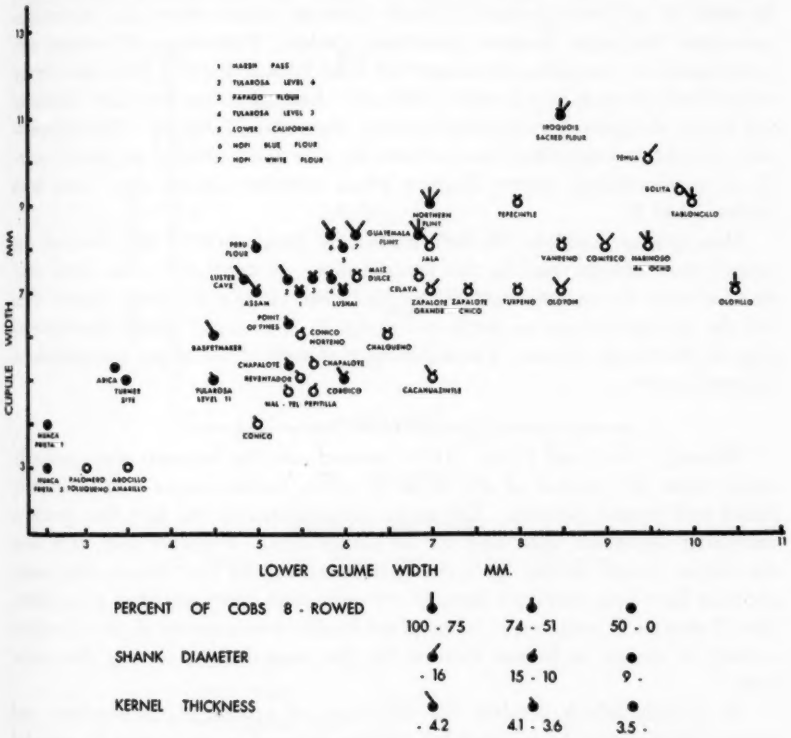
AVERAGE VALUES OF FIVE MORPHOLOGICAL CHARACTERS FOR TWENTY-FIVE EXISTING RACES OF MAIZE IN MEXICO (DATA FROM WELLHAUSEN *ET AL*, 1951, 1952).

(Measurements in mm. except where otherwise indicated.)

Name of race	Cupule width	Width of lower glume	% cobs 8-rowed	Shank diameter	Kernel thickness
Palomero Toluqueño	3.0	3.0	0	8	2.8
Arocillo Amarillo	3.5	3.5	0	8	2.5
Chapalote	5.5	5.5	20	9	4.1
Nal-Tel	5.0	5.5	20	7	3.9
Cacahuazintle	5.0	7.0	0	10	5.2
Harinoso de Ocho	8.0	9.5	100	14	4.4
Olotón	7.0	8.5	20	17	6.0
Maíz Dulce	7.0	6.0	0	11	4.0
Cónico	4.0	5.0	0	8	3.6
Reventador	5.0	5.5	20	8	3.6
Tabloncillo	9.0	10.0	90	11	4.3
Tehua	10.5	9.5	0	21	3.9
Tepecintle	9.0	8.0	0	10	3.7
Comiteco	8.0	9.0	0	22	4.5
Jala	8.0	7.0	0	34	4.6
Zapalote Chico	7.5	7.5	20	13	3.6
Zapalote Grande	7.5	7.0	0	18	3.8
Pepitilla	5.0	5.5	0	12	3.5
Olotillo	7.5	10.5	90	10	3.9
Tuxpeño	7.5	8.0	20	13	3.7
Vandeño	8.5	8.5	0	13	3.6
Chalqueño	6.0	6.5	0	10	3.9
Celaya	7.5	7.0	20	9	3.9
Cónico Norteño	6.0	5.5	0	11	3.5
Bolita	9.0	10.0	50	9	4.1

an accidental deposition, or it may have been buried in an old layer or brought to a recent one by rodents, pot hunters, or a recent occupant of the site. To minimize these effects, arithmetic averages of the measurements of each character have been computed for each sample. Alava (1952) pointed out that such a technique provides the only safe basis for studying variation between different varieties of plants.

Table I lists the average values for each of the characters of each sample studied. Ear shape contributed two columns, one for straight ears and one for tapered ears, thus giving a total of nine characters in which to compare variation. A pictorialized scatter diagram of these same results is presented in text-fig. 2.



Text-fig. 6. Pictorialized scatter diagram of material from Tables I and II showing relationships between variation in five different cob characters among the twenty-five races of maize in Mexico (data of Wellhausen *et al*, 1951, 1952) and the twenty-three samples of the present study. Each dot represents the average measurements of five characters for all maize cobs studied in that group; horizontal axis, width of lower glume; vertical axis, width of cupule; three other characters are diagrammed by rays as explained on the figure. Further explanation in the text.

Text-figs. 3, 4, and 5 show the variation and relationships of these same nine cob characters within each sample of cobs. The method of construction, as well as the general usefulness and reliability of these diagrams, is further discussed below.

An attempt was made to compare the results of this investigation with those obtained by Wellhausen *et al* (1951, 1952) for races of maize in Mexico. Several of the major characters employed in the present study were not employed by Wellhausen and his co-workers. However, their paper contained excellent diagrams of cross-sections of ears of each race drawn to scale; it was possible to make certain measurements directly from these diagrams. Lower glume width in mm. was measured at the widest point indicated on the third concentric circle of each ear diagram. Cupule width in mm. was measured as a straight-line distance across the bases of any two consecutive kernels from the points where their boundaries intercepted the rachis diameter (innermost circle). Percentage of 8-rowed ears was obtained by comparing the number of rows in each drawing with the average values listed for each race in their Table 15. Average values for shank diameter and kernel thickness were obtained directly from their Table 15. The information obtained is summarized here in Table II; it is also presented as part of text-fig. 6, a pictorialized scatter diagram which compares related data from both Tables I and II.

Male spikelet variation has been studied by Alava (1952) for seven of the twenty-three samples used in this investigation. A crude index has been constructed after the manner outlined by Anderson (1936) for both Alava's data and the appropriate data set forth in text-fig. 2. Text-fig. 7 shows the relationships of these index values. The significance of each of the above comparisons is discussed below.

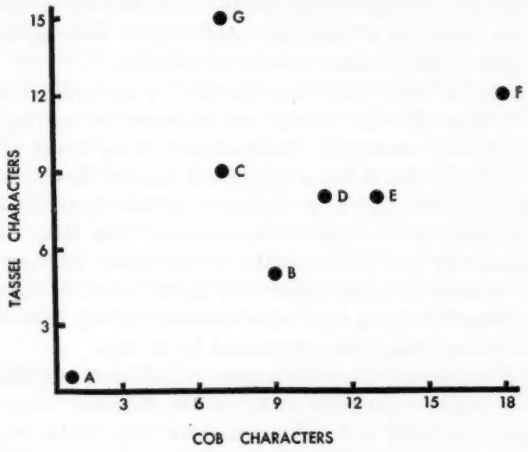
DISCUSSION

Whiting (1944) and Cutler (1951) pointed out that botanists alone probably cannot solve the problem of the origin of maize, because maize is so intimately linked with human cultures. This point is emphasized by the fact that maize is completely dependent upon man for its preservation. Whatever may have been the original factors leading up to this novel situation, the fact remains that maize and man have been associated together for quite some time, and that a consideration of changes in maize types in any given locality over a period of years involves a study of changes in human cultures for that same locality during those same years.

In a study which involves the disciplines of ethnology, archaeology, and botany, caution must be exercised lest theories proposed in one science be regarded as proven facts by workers in another. Since the present investigation has been conducted from the standpoint of botany, such conclusions as can be drawn should depend in so far as possible upon botanical evidence for their support. To this end, botanical information is discussed first, and an attempt is then made to relate this discussion to known facts of ethnology and archaeology.

Botanical Aspects of Maize Cob Analysis

Variation among races of maize is nowhere better illustrated nor more difficult to describe than that found among female inflorescences, or cobs. Within any race, many cobs possess characters the measurements of which lie well within the range of variation of the same measurements from several other races. This exasperating fact is true for all the characters used in this study. Using any one cob character at a time, it is nearly impossible to distinguish races of maize; it is for this reason that the empirical classification of maize by kernel types proposed by Sturtevant (1899) is not of much value to modern maize breeders. Mangelsdorf and Reeves (1939) used evidence from several sources to characterize maize from different parts of the New World. Anderson (1946, 1947a), Anderson and



INDEX VALUES

MAIZE	RACE	COB CHARACTERS	TASSEL CHARACTERS
A	ARICA	1	1
B	ASSAM	9	5
C	CHAPALOTE	7	9
D	PERU FLOUR	11	8
E	GUATEMALA FLINT	13	8
F	NORTHERN FLINT	18	12
G	PAPAGO	7	15

Text-fig. 7. Scatter diagram of index values of seven races of maize in which both the tassel (male inflorescence) and the cob (female inflorescence) have been investigated. Horizontal axis, index values derived from cob study; vertical axis, index values derived from tassel study. Further explanation in the text.

Cutler (1942), Mangelsdorf and Smith (1949) and Wellhausen *et al* (1951, 1952) have used an increasing number of subtler characters in distinguishing both modern and prehistoric races of maize.

Pictorialized scatter diagrams (Anderson, 1949b) are a means by which several such variable characters can be considered at once, thereby emphasizing consistent and typical differences as well as similarities among the particular entities involved. Methods by which a pictorialized scatter diagram is developed are explained by Anderson (1949b, 1952) and Anderson and Gage (1952). Anderson (in press) has discussed the biological and mathematical criteria upon which pictorialized scatter diagrams are based. The value of such diagrams has been emphasized by Stebbins (1952), who considered the method "by far the best yet devised for making the observer aware of a pattern of variation in respect to three or more characters which are varying simultaneously." He also stated (1952) that the method "has the advantage of being repeatable and of focusing the attention of the observer upon certain essential features of variation."

The data listed in Table I have been plotted as a pictorialized scatter diagram (text-fig. 2) to show how the several cob characters are varying and to what extent their variation is correlated. Measurements of depth and width of cupule were chosen as abscissa and ordinate respectively because they varied consistently within each sample (text-figs. 3, 4, 5), could be ascertained from fragmentary cobs, and were susceptible to accurate measurement. The other seven characters were then indicated by rays from each dot of the scatter diagram. Extremes of each character tending to be associated with higher values of cupule width and depth were represented by long rays, while extremes tending to be associated with lower ordinate-abscissa values were represented by no rays.

Several facts concerning the maize samples studied were immediately apparent. At one extreme (upper right-hand corner of the diagram) were predominantly straight 8-rowed cobs with wide, shallow cupules, large rachis-flaps, wide lower glumes, heavy shanks, and thick or moderately thick kernels. This complex of characters was found in Northern Flint and Iroquois Sacred Flour; occurrence of endosperm as flinty or floury is dependent upon a single gene and is therefore of no significance here. These results agreed with those found by Brown and Anderson (1947) for typical Northern Flint varieties; the same complex was identified by Carter and Anderson (1945) as the Eastern complex. At another extreme (lower left-hand corner of the diagram) were cigar-shaped cobs with high row numbers, narrow deep cupules, small rachis-flaps, narrow lower glumes, small shank diameters, and thin kernels. These characters were associated in prehistoric maize recovered at Huaca Prieta, Peru, and Arica, Chile. It is significant that the majority of cobs were essentially complete but only about 5 cm. long. As a whole, these samples were remarkably homogeneous (text-fig. 3). Existence of a third extreme (middle left area of the diagram) is indicatd by tapered cobs with high row numbers, extremely deep cupules, little rachis-flap development, wide lower glumes, medium shank diameters, and thick or moderately thick kernels. The two

maize samples from Asia were responsible. Cobs studied were those grown by Stonor in Asia; varieties involved were described by Stonor and Anderson (1949).

The most striking features of the Asian corn cobs were their extremely deep cupules and their particular form of sclerenchymatization. The rachis tissue and lower glumes of all Asian cobs studied were quite hard, but their hardness was not identical with that of "bony" rachis tissue described by Mangelsdorf and Smith (1949) in connection with teosinte introgression. Whatever its cause, the end product was an extremely stiff, light-weight bulky cob. Studies by Lenz (1948) did not indicate that cell wall thickness had much to do with degree of sclerenchymatization among various races of maize. A deep cupule could possibly be interpreted as a condition which showed little if any "Tripsacoid influence" (Cutler, 1946). An inference cannot be drawn that all Asian maize varieties are alike in this respect, but for both Assam and Lushai samples, this conclusion seems justified.

The nine characters employed in constructing text-fig. 2 showed a strong tendency for association at both extremes. A strong overall association between all sample averages as well as within each sample is clearly shown by comparing the average of any sample in text-fig. 2 with its appropriate population diagram in text-figs. 3, 4, or 5. Individual cobs in the upper right-hand area of each population diagram consistently showed more and longer rays than did those from other parts of the same diagram. This similarity of separation patterns in the several diagrams emphasizes the fact that those limits employed in separating sample averages, while originally chosen in a subjective taxonomic fashion (Stebbins, 1952), were also working within each sample in such a way that morphological trends associated with a particular race of maize were associated with each other.

The diagram as constituted contains samples of rather diverse races of maize; closeness of position on the diagram and similarity of glyphs indicate similar morphology but do not necessarily imply close relationship. Weatherwax (1936) stated that no sound basis exists for any attempt to trace maize origin by arranging varieties from different localities in an evolutionary sequence. Introduction of the dimension of time in the form of archaeological material, however, allows the investigator to arrange maize varieties of both present and past according to cultural succession; the result may or may not be an evolutionary sequence, but such an arrangement is the strongest means available for documenting maize history and has therefore been employed in this investigation whenever possible.

Results obtained in this investigation are compared below with those obtained in three other independently conducted investigations. A high degree of correlation is found in each instance, a fact which indicates a basic soundness in methods employed for cob analysis in this investigation.

Brown *et al* (1952) have discussed relationships among three varieties of Hopi maize, two of which, Hopi White Flour and Hopi Blue Flour, were included in the present study. These workers found that the two varieties had certain re-

semblances to Basketmaker and Eastern maize as well as to each other. Unfortunately, it was not possible to obtain a large enough sample of Kokoma, the variety they reported as resembling Basketmaker most closely, to warrant its inclusion here. Text-fig. 2 indicated that Hopi Blue Flour was basically similar to Basketmaker, differing in cupule width, wide lower glumes, heavy shanks, and presence of 8-rowed cobs. It should be noted that there has been no change in cupule depth and predominance of cigar-shaped ears in development of Hopi Blue Flour from Basketmaker maize.

Hopi White Flour was found by Brown *et al* (1952) to contain an admixture of both Eastern and Mexican germ plasm. The Mexican complex (Carter and Anderson, 1945), known to be present on the Mesa Central of Mexico, is characterized by strongly tapered cobs with high row numbers, thick kernels, and small shanks. This conclusion was borne out by text-fig. 2, which showed Hopi White to have all the characters associated with the Eastern complex with the exception of row number and cob shape; tapered cobs of high row number may be attributed to Mexican influence. Cobs of these two Hopi Flour maizes differed from each other in cupule depth (text-fig. 2 indicates this to be the strongest character contributed by the Eastern complex), cob shape, shank diameter, rachis-flap height, and row number.

In the correlation between results obtained in the present investigation and those of Wellhausen *et al* (1951, 1952) which are listed in Table II, the number of characters used was less than the number employed to separate the samples listed in Table I; yet, a pictorialized scatter diagram (text-fig. 6), using five measurements, presented essentially the same variation pattern as did text-fig. 2, in which nine measurements were employed. It should be noted that the basic pattern of maize cob variation was not altered by using measurements of a different character for the abscissa of text-fig. 6 than that employed in text-fig. 2. If a sample on text-fig. 6 has any real affinity to races with which it may be allied on other grounds, the fact should be shown by its position on the diagram. Text-fig. 6 should also lend further confirmation to the genealogies postulated by Wellhausen *et al* for several hybrid races of maize. That these confirmations are indeed possible was shown quickly and easily. The four races classified by these workers as Ancient Indigenous Races (Palomero Toluqueño, Arocillo Amarillo, Chapalote, Nal-Tel) were closely grouped; moreover they were all placed in the lower left-hand corner of the diagram and all had few to no rays. Thus their characters of small cupules, narrow lower glumes, high row numbers, thin kernels, and small shanks, all believed to indicate primitiveness in relation to other races of maize here considered, were strikingly indicated by text-fig. 6.

Three of the four races classified as Pre-Columbian Exotics (Cacahuazintle, Harinoso de Ocho, Olotón, Maíz Dulce) formed a consistent graded series along the lower edge of the upper region of text-fig. 6. They were placed in a separate class because of their antiquity and resemblance to South American maize. While

the class was somewhat artificial, the positions of three of its four constituents on the diagram in a nearly perfect ascending order indicated a basic similarity in variation pattern.

From these races a group of thirteen Prehistoric Mestizos and a group of four Modern Incipient races were thought to have arisen. For many of these, Wellhausen *et al* compiled a chart showing the two putative parents of the particular race under discussion. Out of a total of eleven genealogical relationships involving other races plotted on text-fig. 6, seven were found to be borne out by diagram position, being for the most part midway in both position and number of rays. These genealogical relationships as postulated by Wellhausen *et al* are listed below. Group 1 is comprised of those races whose positions on text-fig. 6 offered further proof of relationship to their putative parents. Group 2 is comprised of those races whose positions on text-fig. 6 did not approximate positions between their putative parent races.

GROUP 1

Cónico	Palomero Toluqueño	×	Cacahuazintle
Zapalote Chico	Nal-Tel	×	Tepecintle
Chalqueño	Cónico	×	Tuxpeño
Cónico Norteño	Celaya	×	Cónico
Bolita	Zapalote Chico	×	Tabloncillo
Tuxpeño	Tepecintle	×	Olotillo
Comiteco	Tehua	×	Olotón

GROUP 2

Zapalote Grande	Tehua	×	Zapalote Chico
Vandeno	Tuxpeño	×	Zapalote Grande
Celaya	Tabloncillo	×	Tuxpeño
Jala	Tabloncillo	×	Comiteco

The fact that a majority of such genealogies can be substantiated by arranging data obtained from the cobs alone is added proof that races may not only be recognized by cob characters, but that their histories can also be ascertained in the same manner with a high degree of accuracy. It should also be borne in mind that data for the Mexican samples represented averages determined from 3–5 cobs of each race; the accuracy might well have been increased had more cobs been used in determining average values. Text-fig. 6 further showed that variation in Mexican maize followed the same general pattern of character association as did variation among the samples employed in this investigation, and that prehistoric North and South American samples were close to the primitive Mexican races.

Spikelet variation in *Zea Mays* was studied by Alava (1952), using methods which, while applicable to male inflorescences, were of no use in the investigation of maize cobs. Thus if any correlation between results of two independently conducted investigations should exist, it would not only be further substantiation for validity of methods employed and results obtained, but also would indicate that cob and tassel analyses yield comparable results. Similar material from seven different races was examined in each investigation. A numerical index (Anderson,

1936; Stebbins, 1952) for both cob and tassel characters was computed for each race. While admittedly a crude indicator of morphological characters, numerical indices are valuable for summarizing diverse data in a manner which permits direct comparisons to be made. Text-fig. 7 shows the extent of this correlation. Arica had the smallest value in both indices, and there was a general progression toward the upper right-hand corner of the graph occupied by Northern Flint. Papago appeared somewhat aberrant as far as tassel index was concerned, but came closest to Chapalote, a related race, in both values. Peru Flour and Guatemala Flint were close, a further expression of their presumed relationship to one another. Guatemala Flint was closer to Northern Flint for cob-index value. Although a considerable number of units away, Asian material was closest to Arica in both cob and tassel values. Thus with the possible exception of Papago, in which variation is unique but consistent with its past history, the samples showed high correlation between tassel and cob morphology in distinguishing races of maize.

Maize Cob Analysis in Relation to Ethnology and Archaeology

Knowledge of ancient peoples is in large part built upon a detailed study of their refuse heaps; rubbish being what it is, a place is assured for the botanist in archaeological analysis. Analysis of maize remains is especially helpful, since few other plants have become so closely associated with man to the extent that they are reliable indicators of his early history in many parts of the New World.

SOUTH AMERICA AND ASIA

Lowie (1940) pointed out that it was a common mistake to identify all early agriculture with maize. Sauer (1952) contended that seed-crop agriculture was developed after a root-crop agriculture which involved vegetative propagation only. Excavations in northern Chile (Bird, 1943), and more especially in Peru (Bennett, 1948; Bird, 1948), showed that there were indeed agricultural communities without maize. Layers of middens at Huaca Prieta, Peru, beginning about 4000 years ago, contained squash, beans (4 types), chili peppers, *Canna*, cotton, and bottle gourds (*Lagenaria siceraria*, Whitaker and Bird, 1949). Maize did not appear until 850 B.C. Whitaker (1948) pointed out that it is extremely difficult to account for the bi-hemispheric distribution of *Lagenaria*, as it is presumed to be of Asiatic origin. Partly on such distributional patterns, Carter (1950) postulated pre-Columbian contacts between the Old and New Worlds, a theory also put forward by Stonor and Anderson (1949) and Sauer (1952). That it was quite possible to sail in either direction across the broad expanse of the Pacific has been amply documented by Buck (1938).

Another odd fact about prehistoric plants of west-coast South America is that they are presumed to be native to Central America. Either these plants reached the coast as articles of trade among established peoples, or they were taken there by the first settlers of the area, who either came from or passed through the Cen-

tral American region. It does not seem possible that maize would have been overlooked by these peoples as a crop plant had they passed through an area in which it was growing or being grown. Yet evidence on the possible antiquity of maize in central Mexico was recently reported by Barghoorn (1952). Maize pollen has apparently been recovered from sedimentary deposits under Mexico City which may antedate human occupation. Recently, however, the date of human occupation has been pushed back to 9000 years in the same area (Richards, 1953).

A type of maize hitherto not mentioned in this investigation is that which is generally referred to as popcorn. True pops are generally of quite primitive morphology (Mangelsdorf and Smith, 1949). Prehistoric Arica and Huaca Prieta maize remains may quite possibly be those of popcorns; Wissler (1945) showed that this is true for some whole maize ears excavated at Arica. In ear shape and size and in tassel characters (Alava, 1952), these prehistoric remains were comparable to a modern pop variety collected by Parodi in Argentina. They may also be related rather closely to Asian types, since they had deep cupules, high row numbers, and some tapered cobs. Tassel analysis (Alava, 1952) also showed an Asian similarity. The above evidence is suggestive, but it also indicates the necessity for more data before the history of maize in both South America and Asia can be considered to be completely known.

THE AMERICAN SOUTHWEST

Maize in the American Southwest has had a long and complicated history. Man was present in the area 10,000 years ago (Wormington, 1949; Johnson, 1951) but there was little evidence that the area was under continuous occupation from that time until the advent of agriculture. Randolph (1952) stated that an apparently humid and subtropical climate existed there 5,000–10,000 years ago, and that the area itself could be the original home of maize. Carter (1945) likewise postulated the Southwest as a center of agricultural dispersal. All known archaeological remains which contain maize are younger than 5,000 years, so the problem at present is to evaluate the evidence at hand. It should be kept in mind that whatever statements are made below are subject to revision in the light of further discoveries.

Carter and Anderson (1945) noted three major cultural provinces in the Southwest: Hohokam, Mogollon, and Anasazi (Puebloan). At the time of their survey, little was known of the Mogollon civilization, but recent excavations at Tularosa and Cordova Caves (Martin *et al*, 1952) have produced evidence establishing this cultural province as one of equal importance with Hohokam and Anasazi. Archaeological maize is now known for each of the three cultural provinces. Hohokam maize was found in Ventana Cave, Arizona (Haury, 1950). It is similar to but not identical with modern Pima-Papago varieties (Carter and Anderson, 1945). Chapalote, an ancient Mexican race, is today found in northwestern Mexico, an area which was also part of the Hohokam cultural province (Amsden, 1949). Relationships between Papago and Chapalote have been dis-

cussed above. Since the Hohokam area was relatively isolated from influences of neighboring cultural patterns, the maize found there today is much the same as it was in ancient times. It is reasonable to assume that prehistoric maize in this cultural province was similar but not identical to that of Basketmaker and Mogollon cultures, and that modern Papago and Chapalote were derived from it. It was shown (text-fig. 2) that maize remains recovered from Tularosa Cave Level 11 were quite similar to both Chapalote and Basketmaker. Similarity between Chapalote and Basketmaker II maize from Cottonwood Cave (Hurst, 1948; Hurst and Anderson, 1949) was pointed out by Wellhausen *et al* (1951, 1952). Amsden (1949) noted the similarity of modern Papago to Basketmaker, as did Carter and Anderson (1945). The present investigation showed that Basketmaker resembled Chapalote much closer than it did Papago, but the important point is that all three cultural areas, Hohokam, Anasazi, and Mogollon, had at an early date maize which was variable but essentially similar. Maize of the Hohokam area remained relatively unchanged; that of the other two areas was strongly influenced by maize from more remote places. Text-fig. 5 illustrates the variable nature of early southwestern samples. In contrast to maize of the Southwest, remains from Arica, Chile, and Huaca Prieta, Peru, are very homogeneous; furthermore, maize of these two areas (American Southwest and South American West Coast) were contemporary. Explanation of the variability in the one location and homogeneity in the other at the same time is but one of the many problems of maize history.

Basketmaker maize was widespread, having been reported from several sites in the Anasazi area. Some of the better known sites are Cottonwood Cave, western Colorado (Hurst, 1948; Hurst and Anderson, 1949), Mummy Cave, Cañon del Muerto, Arizona (Anderson and Blanchard, 1942), and Painted Cave, northeastern Arizona (Haury, 1945). Basketmaker-like maize was reported outside the Anasazi area by Brown and Anderson (1947) in prehistoric remains of rock shelters and caves from the Ozarks to southern Ohio.

Two combinations of maize characters, one peculiar to the Mexican Mesa Central and the other to the eastern United States, were superimposed in varying amounts on southwestern maize. The spread of each influence may be traced by analysis of successive samples; in such work, the importance of dated maize remains can hardly be over-emphasized. Mexican influence is characterized by strongly tapered cobs with high row numbers (Carter and Anderson, 1945), thick kernels, and small shanks. This type entered the Southwest from the Northeast rather than from Mexico directly; its greatest influence has been found in remains of the Fremont Basketmakers of Yampa Canyon, Utah, dated at 400–800 A.D. (Burgh and Scoggin, 1948).

At Luster Cave, in extreme eastern Utah, maize was subjected to strong Eastern influence prior to 1000 A.D. Text-fig. 2 showed this sample to be closely related to Hopi White Flour among ethnological races examined in this study. Hopi White Flour differed, however, in being more extreme for certain Mexican (tapered

ears, high row numbers) and Eastern characters (large shanks, wide lower glumes). Maize from the Davis Site (Newell and Krieger, 1949) was analyzed by Jones (1949) and found to be entirely Eastern. These maize remains were dated at about 700 A.D. by Jones and at about 400 A.D. by Johnson (1951).

The question of origin of Eastern influence has long been a puzzling one. Anderson (1947a) and Brown and Anderson (1947) presented evidence that Eastern maize is related to Guatemalan maize. Jones (1949) reported that he and Krieger independently reached the conclusion that both maize and pottery types recovered at the Davis Site bore a resemblance to those of Guatemala. Carter (1946) suggested that maize could have been carried up the east coast of Mexico or across the Gulf to southern United States. Regardless of the method employed, this movement must have taken place in time for the influence to have been carried to the Southwest by 1200 A.D., a date which Carter and Anderson (1945) recognized as closely approximating its first appearance in that region. Judson (1951) called attention to the fact that a great drought occurred in the Southwest in 1276–1299 A.D., and that many Indian tribal migrations took place around that time. The direction of movement of maize into the Southwest was from east to west; Carter and Anderson (1945) noted that among the present-day Puebloan tribes, those of eastern pueblos have more eastern-like maize than do those of western pueblos. It is generally accepted that there is influence of Plains cultures in the southwestern area. This influence also is stronger in eastern pueblos than in western ones, and is another indication of how well maize history is correlated with the history of the peoples who grew it.

THE AMERICAN SOUTHEAST AND EAST

Wherever the Eastern complex came from, it was probably carried up the river valleys of the Mississippi and its tributaries by Indian tribal migrations. A date of 900 A.D. was assigned to the earliest known Burial Mound I culture by Ford and Willey (1941), who also identified the beginnings of horticulture in eastern United States at this time. Burial Mound I peoples were in turn supplanted by Burial Mound II and later (1200–1400 A.D.) by Temple Mound I and Temple Mound II cultures. Ford and Willey derived the Iroquois culture of New York from a welding of these four intrusions onto an archaic hunting-gathering population; they considered that this and other allied upper Mississippian cultures reached a peak after 1500 A.D., and lasted until historic times. Although other evidence has been presented in support of the idea that maize was a late arrival in eastern woodland cultures (Linton, 1924; Kroeber, 1939), from a botanical point of view the postulated time of arrival of maize in this area appears too recent. This impression is strengthened by consideration of the length of time the same type of maize was present in the Southwest.

Recent radiocarbon dating (Johnson, 1951) indicated that Mississippi valley and other eastern cultures were of greater antiquity than had previously been

thought. Johnson (1951) reported that Hopewell sites from Ohio and Illinois were about 1000 years older than had previously been estimated. The whole chronology of the Southeast has become unsettled because of radiocarbon dating results, but the presence of cultures in this area at earlier dates further strengthens the idea that maize is of greater antiquity than had been thought possible, and opens a way to minimize a long-standing inconsistency between archaeological and botanical evidence.

Since there was, as Ford and Willey (1941) and Waring and Holder (1945) pointed out, a suggestion of strong Mexican influence in Temple Mound I and II cultures, the idea would be greatly substantiated should remains of Mexican maize ultimately be found in excavations. Botanical evidence exists that maize of the Southeast is related to a Mexican Gulf Coast race (Wellhausen *et al*, 1951, 1952), and hybridization of this Mexican maize with eastern flint maize already present in the Southeast probably resulted in the variable forms called Southern Dents by Brown and Anderson (1948).

Northern Flint and Southern Dent maizes were subsequently brought together to form modern hybrid corn-belt maize (Anderson and Brown, 1952a, 1952b). A significantly large collection of Southern Dents was not available for inclusion in the present study, but the few available cobs which were studied showed a rather close resemblance to Northern Flints in cob characters. Evidence that many Southern Dents were intermixed with Northern Flints was presented by Brown (1949), who studied chromosome knob numbers in United States maize. He found Northern Flints to have the lowest knob numbers, Southern Dents the highest, and corn-belt forms intermediate between these extremes. Longley (1938) had previously surveyed Indian maize varieties from the United States and northern Mexico. He reported the same general rise in knob number among southeastern varieties. He also found that maize of Arizona and New Mexico was high in knob number. Carter (1949) used knob numbers on chromosomes of Indian maize to indicate tribal affinities and differences. The fact that such an investigation yielded results substantially the same as those of different approaches is another example of how closely maize mirrors the history of those with whom it is associated.

An important point regarding use of Northern Flint and Southern Dent maizes in corn-belt maize production is that the hybrid vigor manifest in this cross is based upon small differences between two already-intermixed races. This situation may possibly indicate that improvement of maize by hybridization techniques has barely begun. Since identification and classification of races are becoming a necessary part of maize breeding, a knowledge of cob variation should be of practical value in the development of new strains of hybrid maize. The principles of cob analysis set forth above, even though they employed small morphological differences, may be considered fundamentally sound, because results obtained from their analysis were in agreement with ethnological and archaeological as well as botanical data of other workers.

Summary

Morphological characters present in the female inflorescence, or cob, of *Zea Mays* L. have been measured on over 500 cobs representing both modern and archaeological varieties. External characters measured included row number, shank diameter, cob diameter, and over-all cob shape. Internal characters measured included cupule width, cupule depth, height of rachis-flaps, kernel thickness, lower glume width, rachis diameter, and pith diameter.

Analysis of pictorialized scatter diagrams of averaged measurements showed a high degree of association of these characters. These results agreed closely with those of previous investigations employing other methods. The results of archaeological maize analysis were in harmony with previous conclusions based on purely archaeological data. Such agreements indicate the validity of cob analysis for characterizing variation in races of maize.

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THE CYTOLOGY, MORPHOLOGY, AND SYSTEMATIC RELATIONSHIPS OF *DELPHINIUM* × *BELLADONNA* HORT. *EX* BERGM.*

MARILYN AMY GAGE

I. Introduction

Among the cultivated perennial Delphiniums the problem of the origin of the forms variously termed "garland larkspurs" (Bailey, 1930) or *Belladonna* types has been raised more than once. The group as it is known at present includes not only *Delphinium* × *Belladonna* Hort. *ex* Bergm., but at least the 45 variants listed by the Royal Horticultural Society (1949), and probably certain other hybrids of unknown origin some of which are no longer in cultivation but were recorded in the literature of the last century.

Two main theories have been proposed regarding the nature of the assemblage. (1) L. H. Bailey, following the example of Huth (1895), the last monographer of the genus, considered these plants to be forms of *D. cheilanthum* Fisch. var. *formosum;* his grounds are wholly morphological. (2) Lawrence (1936), on the other hand, has suggested that *D. Belladonna* originated in gardens as a triploid hybrid between a tetraploid species and a diploid species, and that subsequent doubling of the chromosome number resulted in the fertile line now in cultivation. His hypothesis is in line with the known facts, for until early in the present century *Belladonna* was quite sterile and was propagated wholly vegetatively; moreover, the present fertile strain is a hexaploid.

In studying the origin of cultigens the historical method alone is obviously inadequate. Students of cultivated plants are well acquainted with the hazards of attempting to place even well-known species into conventional taxonomic categories. Even with such a relatively recent variety as *D. Belladonna,* caution is necessary in considering historical references, for it often happens that opinions given in early descriptions are contradictory or suggest some parentage which, in the light of present knowledge of cytology and genetics, is far from the truth. One can accept, with caution, species listed in cultivation at a certain period, but there must always be the reservation that morphologically similar species are subject to confusion, and that any of these species may, and probably do, differ from their wild relatives as a result of horticultural "amelioration."

Morphological comparisons with known species have often been used in establishing the possible parentage of plants of unknown origin. This method is most useful in groups where there are clear-cut characters whose extreme and intermediate expressions are easily recognized. The genus *Delphinium* is, however, notoriously variable, and specific distinctions are based to a very great extent upon quantitative differences, such as width of leaf segments, degree of dissection of

* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy. During the last year the study was carried out under a predoctoral fellowship of the National Science Foundation.

the leaves, extent and type of axial branching, degree of incision of the "bee", length of spur, and the like. Every one of these characters is subject not only to genetical, but also, to a high degree, to environmental variability. Therefore, before employing such characters, it is important to understand to what extent each character may be modified by the environment.

A third method of general use in establishing relationships between species, that of cytological analysis, is often more reliable. A number of investigators have shown that degree of relationship between species may often be estimated by studying the morphology and especially the pairing affinities of the chromosomes (see Stebbins, 1950, for a review of the literature). However, where the chromosomes of the parental genomes are not strongly differentiated there must often remain doubt as to the sources of the chromosomes which are pairing in the hybrid. Especially in polyploids above the tetraploid level such problems are intensified by the presence in the same individual of several genomes, so that autopolyploidy and allopolyploidy may coexist.

The relationships of *D. Belladonna* must therefore be considered from a combination of several standpoints, and the solution must be based upon that hypothesis which best makes use of the information obtained by each method.

Of the materials employed in this study, families of various species and hybrids were grown in the experimental greenhouses of the Missouri Botanical Garden and of Washington University, in St. Louis. Herbarium specimens were made available by the Bailey Hortorium of Cornell University and from the collections of the Missouri Botanical Garden.

I wish to acknowledge my indebtedness to Dr. G. A. L. Mehlquist, of the University of Connecticut, formerly Research Horticulturist at the Missouri Botanical Garden, who suggested this problem and who stimulated my interest in it by his own enthusiasm. I am also indebted to Dr. Edgar Anderson and other members of the staff of the Missouri Botanical Garden who have aided me in many ways.

II. Taxonomy and Morphology

A. Natural Species

History of the Genus.—

Since the establishment of the genus in its modern form by Tournefort (1700), *Delphinium* has received various treatments. In his 'Species Plantarum' Linnaeus listed the six species, *D. consolida, D. ajacis, D. peregrinum, D. grandiflorum, D. elatum,* and *D. Staphisagria.* By the close of the eighteenth century only six more species had been added, but in the century and a half since then, the number of species described has increased to more than 300. A. P. DeCandolle was the author of 23 species, and in his 'Prodromus' (1824) he grouped 53 species into the four sections, CONSOLIDA, DELPHINELLUM, DELPHINASTRUM, and STAPHISAGRIA. K. Prantl, in Engler and Prantl's 'Die Natürlichen Pflanzenfamilien' (1888) merged DeCandolle's STAPHISAGRIA and DELPHINASTRUM into one section, STAPHISAGRIA;

and later, modifications were made by others—notably Asa Gray (1887), Robinson and Fernald (1908), and Huth (1895). The most recent treatment of the American species is that of Ewan (1945).

Huth published in 1895 his "Monographie der Gattung *Delphinium*," in which he attempted a natural classification of the 200 odd species treated. He recognizes two subgenera: CONSOLIDA, in which there is a single carpel, the petals are fused into one, and seeds are scaled and three-cornered; and EUDELPHINIUM, in which there is more than one carpel and the four petals are free. Within the second subgenus he distinguishes three sections:

ELATOPSIS—petals deep violet or black, lower petals bifid and bearded.

DIEDROPETALA—petals light, the same color as the sepals or dirty yellow, deeply bifid, lobes acute.

KOLOBOPETALA—color of petals as in DIEDROPETALA; limb of lower petals round or rectangular, entire or bilobed, lobes round or truncate at tip.

Of the species considered here, *D. elatum* L. belongs to the series RACEMOSA of section ELATOPSIS, and *D. grandiflorum* L., *D. cheilanthum* Fisch. *ex* DC., and *D. tatsienense* Franch. are included in the series CHEILANTHOIDEA of section KOLOBOPETALA. While *D. Belladonna* Hort. was not known to Huth, he included as varieties of *D. cheilanthum* several cultigens which are certainly very similar to it.

Further consideration of the taxonomic categories will be restricted to *D. cheilanthum*, since it alone has been confused with *D. Belladonna*. The other species (*D. elatum*, *D. grandiflorum*, and *D. tatsienense*) are taxonomically well-known, and while they include many natural and horticultural variants, there is no problem in determining the affinity of such variants.

Delphinium cheilanthum Fisch. *ex* DC.—

Apart from the question of any direct relationship between *D. Belladonna* and *D. cheilanthum*, a problem which will be discussed later, the two species are confused in herbaria and in gardens, where identifications must be made largely upon a morphological basis. The magnitude of the problem is amply brought out by L. H. Bailey in 'The Garden of Larkspurs' (1939), in which he attempts to trace the history of *D. Belladonna* as a derivative of *D. cheilanthum*. He bases his conclusions upon a comparison of certain historic plates and descriptions of *D. cheilanthum* and of certain horticultural varieties (*D. formosum* Hort. and *D. Hendersoni* Hort.). The last two will be taken up in the next section, and I shall discuss here only *D. cheilanthum* in order to clarify its position, since it is apparently infrequent in herbaria in this country.[1]

Delphinium cheilanthum Fisch. *ex* DC. is based upon a specimen sent to A. P. De Candolle (1818) by Fischer from the region of Doroninsk in Dahuria (in

[1]Bailey (1939) says: "Yet it is strange that *cheilanthum* does not appear as a native plant in the great herbaria to which I have had access. Specimens cited by Huth mostly are plants considered by him to be botanical varieties of *D. cheilanthum*."

trans-Baikal Siberia). In 1819 von Schrank figured and described the same plant (under the name of *D. cheilanthes*) in 'Plantae Rariores Horti Academici Monacensis' (pl. 7). Earlier, in 1769, J. G. Gmelin had described and illustrated in his 'Flora Sibirica' a plant which, according to De Candolle, Fischer had indicated was the same as his *D. cheilanthum*. In 1820 a plant grown near London from seed sent by Fischer was figured in the 'Botanical Register.'

In addition to the sources cited by Bailey, a number of accounts of the species given by collectors in Siberia and northern China (Ledebour, 1842; Regel, 1861; Trautvetter, 1847, 1877a, 1877b; Turczaninow, 1842; Glehn, 1876; Brühl, 1896; and Komarov and Schischkin, 1937) delimit *D. cheilanthum* Fisch. as a species or species complex, with well-defined characters and a distinct geographic distribution. From these accounts, and the Huth monograph, the species may be characterized as follows:

DELPHINIUM CHEILANTHUM Fisch., in DC. Prodr. 1:53. 1824.—Stem tall, simple or branched; leaves glabrous or pubescent (especially on the under surfaces), 5-parted, parts oblong to narrowly lanceolate-acuminate; lower bracts many-parted. Inflorescence racemose to subcorymbose, peduncles bibracteolate; upper bractlets equal to spur. Flowers blue, rarely white; spur straight or slightly curved; sepals ovate, pubescent or puberulent externally; upper petals glabrous, pale yellow or blue, lower petals large, with ovate or subrotund limb, entire or rarely emarginate-bilobed, with yellow pubescence above. Carpels 3, glabrous or pubescent, tips curved at maturity, to 20–25 mm. long; seeds 3-angled, with winged margins, faces scarcely squamate. Flowers in June and July (pl. 9).

A number of varieties have been described, but undoubtedly any future monographer must rework the alliance. The exact limits of the species are still somewhat in question, since Huth describes *Delphinium Middendorffii* Trautv. as a distinct species, although in his natural key to the genus he lists it as a variety of *D. cheilanthum*, distinguished by having the apices of the sepals lanceolate. Moreover, he notes: "*D. Middendorffii* scheint eine verkümmerte Form des *Delphinium cheilanthum* mit verlängerten Kelchblättern zu sein." By 1877 Trautvetter, who originally described *D. Middendorffii* (1847), conceded that it was but another variety of *cheilanthum*, and added (translation):

> "*Delphinium cheilanthum* Fisch. varieties grade into one another and are distinguishable with difficulty. This species possesses sometimes a low stem (var. *Middendorffii*) and sometimes a taller stem; and this latter form has flowers either larger (var. *typica*) or smaller (var. *parviflora*). Indeed, sometimes var. *Middendorffii* has larger, and sometimes smaller flowers, so that sometimes it approaches var. *typica* and sometimes var. *parviflora*."

An American species, *D. chamissonis* Pritz. (from the Bering Sea region and the Yukon valley) is also apparently a close ally of *D. cheilanthum*. Comparing *D. chamissonis* and *D. Middendorffii*, Ewan (1945) says: "All of the more than a score of collections examined show so much variation in spur length and, indeed, flower size as a whole, as to render it difficult to draw any distinction between the two species from these characters."

B. HYBRIDS OF THE BELLADONNA TYPE

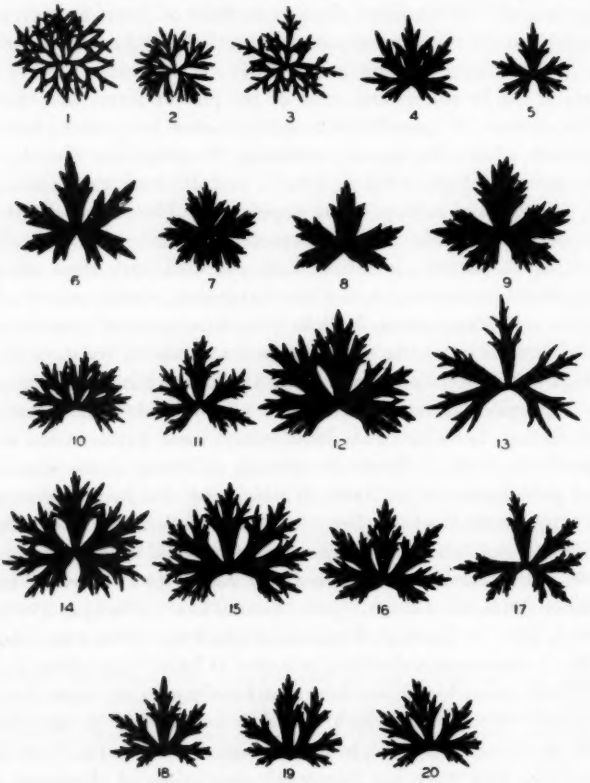
The history of the cultivated Delphiniums is extremely complex (see Wilde, 1931; Bailey, 1939). As early as 1778 *D. elatum* L. and another form listed as *D. azureum* (not *D. azureum* Michx., which was not described until 1803) were offered in the trade, and at least by 1824 *D. grandiflorum* L. (two varieties) was offered. Other species were rapidly introduced and by the middle of the century hybridization was being carried on by a number of French growers, chief among whom was Victor Lemoine, originator of most of the first varieties of perennial garden Delphiniums. English plantsmen were somewhat later in the field, but particularly since the 1870's, when the first varieties of James Kelway were introduced, a large part of the development of new hybrids has been carried out in Britain.

As nearly as can be ascertained, most of the present forms were derived from relatively few species. *D. grandiflorum* and *D. elatum* have chiefly been involved, although hybrids with other species, including *D. tatsienense* Franch. (Lemoine, 1914), *D. cardinale* Hook. (Wilde, 1931), and *D. nudicaule* Torr. and Gray (Lawrence, 1936) have enjoyed some popularity. Horticultural literature has frequently not been reliable regarding species in cultivation, and allies of *D. grandiflorum* or *D. elatum* could have been confused with these species and so have been employed in crosses at a time antedating any existing records of their use.

As has been mentioned above, *D. Belladonna* first appeared some time after the middle of the last century; the earliest known mention of its name is in 'Floricultural Cabinet and Florist's Magazine' for 1857, where it is listed as a desirable form with large pale lavender-blue flowers. In the 1865 catalogue of James Backhouse & Son, of York, England, *Belladonna* is listed and described as "a lovely turquoise, perfectly hardy." There are sporadic references to the plant in various horticultural publications before 1880, in which year the English firm of Kelway introduced it to a wide market. For a long time *Belladonna* was reported to be sterile. However, in 1902 or 1903 a plant grown by G. Gibson, of Leeming Bar, yielded three pods, whose seeds produced five plants, two of which became the named varieties "Mrs. G. Gibson," and "Grandiflora" (Phillips, 1949); and in 1905 Sutton & Sons, of Reading, England, obtained seed from two plants. Thus it appears that a chromosome-doubling occurred at least twice within a few year's time. The fertile strain has always been true-breeding, in the sense that there has been no recovery of anything which resembles any diploid or tetraploid species which might be assumed to have been the original parents (although it will be demonstrated later that weak but measurable associations of characters present in such species are still to be found). It it true, nonetheless, that heterozygosity in these original amphidiploid forms must have been fairly high, judging from the large number of *Belladonna* varieties introduced within the next few years.

It is of interest that the 'Journal of the Royal Horticultural Society' (1907) says of Sutton's first seedlings: "Some . . . resembled *Delphinium Belladonna* very closely, but some more nearly approached *Delphinium formosum*, and one bore

flowers of a very beautiful deep blue tint." *D. formosum* referred to here is the horticultural form and not the species of Boissier and Huet. Like *Belladonna*, it was a garden hybrid of unknown origin, and, also like *Belladonna*, it is said to be a hexaploid (Propach, 1939, 1940; Mehlquist, unpublished). It was first offered in 1855, and according to Van Houtte (1857) it was already fertile. This, coupled with its superficial resemblance to the diploid species *D. cheilanthum*, caused Huth to list it as a variety of that species in his monograph, although it has never been reported in nature (pl. 8). It is suggested that *formosum* may have originated from an early and unrecorded doubling of the chromosome complement of *Bella-*



Text-fig. 1. Leaf types in *Delphinium* species and hybrids (× ¼).

1. *D. grandiflorum* var. *chinensis* Blue Butterfly.
2. *D. grandiflorum* var. *chinensis.*
3. *D. tatsienense.*
4. *D. cheilanthum*, from specimen collected by Karo in Dahuria.
5. *D. cheilanthum*, from plant grown from seed at the Missouri Botanical Garden.
6–9. *D. elatum*, showing range of variation.
10–15. *Belladonna* types: 10, Lamartine; 11, Smith's *Belladonna.*
16–20. Experimentally produced triploids: 16, 50-15-3; 17, 50-40-2; 18, 48-27-4; 19, 48-27-6; 20, 48-27-10.

donna, or at any rate that it originated in the same manner as *Belladonna*. Certainly, there are no consistent differences between the two.

The following is a general description of *D. Belladonna:*

DELPHINIUM × BELLADONNA Hort. *ex* Bergm.[2]—Racemose open-flowered perennial with simple or branched stem up to 1.5–2.0 m. tall; herbage pubescent or glabrous; leaves palmate or deeply 3-parted and strongly ribbed, the parts again divided or lobed, the degree of dissection of the parts gradually increasing from rosette leaves to bracts, the main division of the stem leaves narrow-cuneate to narrow-oblong, 0.2–2.0 cm. broad at base, the petioles nearly or quite as long as the blade. Inflorescences of relatively short and open (5- to 20-flowered) racemes, the peduncles with parted bracts at base and the pedicels usually long, with basal simple bracts and paired short bracteoles immediately subtending the flowers. Flowers large, single, occasionally semi-double, mostly light to dark blue and somewhat declined; sepals thinly pubescent outside, blunt; spur about equalling the sepals and straight or somewhat curved at the end; petals mostly white or light-colored, bearded with yellow, making a large "bee" which fills the throat of the flower. Follicles 3, pubescent or glabrous, up to 2.0 cm. long, the apex curved; seeds 3-angled with somewhat winged margins, not squamate. Flowering period prolonged by the production of successive shoots during the growing season (pl. 8).

Another variety of interest, Lamartine, originated with the French house of Lemoine & Son in 1903. Like *Belladonna*, it was at first sterile, and the present fertile strain had its origin in 1916-17 when doubling of the chromosome number apparently occurred among some plants growing at the Royal Moerheim Nurseries in Holland (Lawrence, 1936). The parentage of this variety is also obscure. In answer to my inquiry, the present head of the firm replied that they had no record of its antecedents, but that experimental work had suggested that the parents might have been an *elatum* type (*sic*, Pacific Giant) and *D. grandiflorum*. In habit, Lamartine is quite similar to *Belladonna*, being of the same height, with a loose, tapering spike, and fairly numerous lateral branch spikes. The leaves are similarly cut (text-fig. 1). The flowers are long-spurred, with sepals ultramarine suffused with purple, and the petals are dark-edged, shading to white, with a yellow beard. Like *Belladonna*, it has an extended blooming period.

There are also grown at present two triploid varieties, *Moerheimi* and Capri, which, while not directly related to *Belladonna*, have a close morphological similarity to that variety. The most complete and authoritative account of these triploids is that given by B. Ruys of the Royal Moerheim Nurseries (1911):

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[2] *D. Belladonna* Hort. is equivalent to *D. Belladonna* Bergm., listed in 'Index Kewensis.' Bergmans, who published his binomial in 1925, is among those who believe the plant to have originated from a cross between *elatum* and *cheilanthum*. He lists no sources for his opinion.

> "For about twenty years I have been interested in white Delphiniums and have purchased all the light-colored novelties which I could obtain, with a view to crossing them with large-flowered, light-blue varieties of strong constitution . . . [A few years ago] I found in a batch of seedlings one plant with five spikes. Of these, two spikes bore pure white flowers, two bore blue flowers, and some parti-colored, half-blue, half-white flowers. Next year, when the five divided plants flowered, I noticed that two had only white flowers, two only blue flowers, and one plant had some flowers white and others blue, whilst still others were half white and half blue."

Both the white and the blue variety were propagated and marketed, the former under the name of *Moerheimi,* and the latter as Capri. Aside from the color, there is no single definitive character to separate these and *Belladonna,* although, as mentioned above, these varieties are triploid.

In addition to the present-day varieties of the *Belladonna* type, a study of the literature reveals that other hybrids of similar appearance were known in the last century, though they have now passed from cultivation. Because of their bearing upon the possible constitution of *D. Belladonna,* some of these early hybrids are described below:

The earliest recorded *Delphinium* hybrid was *Barlowii,* figured by Lindley in the 'Botanical Register' of 1837. The plant, from a nursery in Tooting, had been received from an establishment in Manchester, and was believed to be the result of a chance cross between *D. grandiflorum* L. and *D. elatum* L. It was reported to be a continuous bloomer. 'Paxton's Magazine' described it the following year:

> "Plant perennial, growing usually from 4–5 feet high. Leaves with 5 principal divisions, deeply lobed and jagged; serrations acute; deep green on surface, light green beneath, smooth. Flowers semi-double, of a most intense blue color, produced very numerously in terminal spikes. Sepals of the calyx greenish externally."

Neither the description nor the Lindley plate, which shows a rather dense spike of semi-double blooms and, in the background, part of a leaf in outline, is complete enough to indicate the affinities of this plant. Moreover, except that the flowers are semi-double in each case, the Lindley plate is quite different from the Paxton plate, which indicates that the plant had a brownish bee, and leaves more deeply incised than those in the earlier plate. Since both plates were drawn from living plants, one is confronted with the alternatives that *Barlowii* was a highly variable variety, or that the two artists had available two quite different varieties. The plant in the earlier illustration might easily belong to the group of hybrids which includes *Belladonna;* the later plate appears, rather, to be merely that of an *elatum* variety. Herbarium specimens of plants sold as *Barlowii* within the last 20 years or so are quite different from either of these, being single dark-blue types, and not different morphologically from *D. Belladonna.*

The next form of interest, *D Hendersonii* Hort. (pl. 7) is of extremely dubious background. It was first mentioned by Moore and Ayres in the 'Gardeners' Magazine of Botany' (1850) and was described under the name *D. cheilanthum* var. *Hendersonii* A. Henfr.:

"Hardy herbaceous perennial with large showy rather distant flowers. Leaves five-parted, lobes oblong or acuminated, trifid or obscurely bi-trifid, 4 inches in diameter, on long petioles; floral leaves three parted, with the lobes broadly linear, acuminated, simple. Racemes axillary and terminal, lax; the pedicels larger than the bracts. Flowers large and showy, ultramarine blue, with veins a little deeper; two lower petals with a roundish ovate limb, obliquely inflexed and whitish in the middle, bearing a yellow beard, slightly irregular on the margins, with a few ciliary hairs at the apex. Ovaries 3, glabrous, green, veined with bluish lines."

The text states that the plant was grown by E. G. Henderson of St. John's Wood, from seedlings purchased from M. Chauvière of Paris.

Lemaire's 'Jardin Fleuriste', of 1851, figures the same plant as *D. cheilanthum* var. *Chauvieri*. Lemaire regarded it as merely a variant of the species, whose distribution and habitat he considered briefly. Quite in opposition to Lemaire, Harrison (1853), describing the same plant, stated: "It was raised by M. Chauvière, nurseryman of Paris, from *D. chinense*, impregnated by *D. elatum-splendens*." This author also noted that *Hendersonii* was a profuse bloomer, of bushy habit, flowering over a long period of time.

Hybrids of known parentage.—

During the past eight years there have been produced at the Missouri Botanical Garden a number of hybrid Delphiniums of particular interest. Several hundred pollinations were made between *D. elatum* and different strains of *D. cheilanthum* and *D. grandiflorum* var. *chinense*, in an effort to find out which, if either, of these hybrids more closely resembled the *Belladonna* assemblage. Up to this time there have been no successful pollinations of *D. elatum* by *D. cheilanthum*. However, the other cross (that between *elatum* and *grandiflorum*) has been successful four times, yielding two families of 3 plants each, one family of 2 plants, and one family of 13 plants.

1. *47-98-3* × *D. grandiflorum* var. *chinense* "Blue Butterfly".—Hybrid Nos. 48-27-1 through 13. (This and the following cross were made by Dr. G. A. L. Mehlquist.)

The seed parent was one of a line of white semi-double *elatum* forms developed by Dr. G. A. L. Mehlquist. The group is exceptional in being the only line of whites in which there has been an approach to homozygosity without concomitant weakening and loss of the line. 47-98-3 had dense spikes borne on the rather short main axes, and leaves of medium size, pubescent, and palmately divided, with relatively narrow segments (pl. 10). The pollen parent, on the other hand, was a low-growing plant with a branched, very open inflorescence of fairly large rich deep blue single flowers in few-flowered panicles. The leaves were relatively small, dull green, glabrous, and finely dissected. This form, too, was true-breeding, and the variety has been grown at least since 1910 when it was among the perennials planted at Wisley (Jour. Roy. Hort. Soc., 1910) (pl. 9 and text-fig. 1). The progeny of this cross included 13 individuals which were generally of intermediate habit and varied very little among themselves. The following description serves to characterize them and point out their chief differences from the parents.

Text-fig. 2. Pedigrees of major lines of triploids and hexaploids.

48-27- Series.—Racemose open-flowered perennials, with simple or usually branched stem up to 1.0–1.25 meters tall; herbage pubescent. Leaves palmate and deeply 5- or 3-parted and strongly ribbed, the parts again divided or lobed, the degree of dissection increasing progressively from the rosette to the bracts, the main divisions chiefly narrow-cuneate, up to about 1.0 cm. broad, the petioles as long as or slightly longer than the blade. Inflorescences not spiciform, the terminal one a 15- to 20-flowered raceme, the lateral of fewer flowers, the peduncles with 3-partite bracts at base and the pedicels with basal simple bracts, and paired bracteoles 0.8–1.0 cm. long subtending the flower. Flowers medium-sized, single, violet and cobalt, on long pedicels and somewhat declined; sepals thinly pubescent outside, blunt, the spur slightly longer than the limb and usually somewhat curved at the end; petals the same color as the sepals, bearded with short golden yellow hairs. Follicles 3, pubescent, not developing into fruits, apex curved. Flowering period prolonged by the production of successive shoots during the growing season (pl. 11 and text-fig. 1).

2. *48-2-3* × *Blue Butterfly.*—Hybrid Nos. 48-6-1 through 48-6-3.

48-2-3, the seed parent of this group, was a selection from Vetterle and Reinelt's

Galahad Series of their Pacific Giant Hybrids. The plant, a white semi-double, was not available to me.

The three hybrid individuals in this group were quite similar to the hybrids described above, the chief differences being the regular production of one or several additional petals of either sort, and the generally larger, less open flowers.

3. *Summer Skies* × *D. grandiflorum (47031-1).*—Hybrid Nos. 50-15-1,-3,-4.

The seed parent of this cross is a selected seedling from the Pacific Giant series, Summer Skies, an *elatum* type with semi-double flowers with sky-blue sepals and white petals in tapering, somewhat dense spikes (pl. 12). It has been found to be true-breeding for color (Mehlquist, unpublished). The pollen parent was from seed obtained from the Royal Botanic Gardens at Kew as *D. tatsienense.* However, determination of the plant, using Huth's key, showed that it must have been, rather, a corymbose variety of *D. grandiflorum.* Numerous attempts were made to obtain seed, but 47031-1 was completely seed-sterile.

The three hybrid individuals of this cross differ in a number of particulars from those of the other crosses, being taller, with a strong main axis which bears lateral spikes in the manner of *D. elatum,* but these more profuse and more strongly developed than in that species. Leaves of 50-15-3 are much like those of the 48-27- series, whereas those of the other two plants are considerably larger and have the ultimate divisions rounded rather than acute. The flowers are again mixed blue and violet (although the blue of these plants is somewhat more brilliant than in the other crosses) and are more or less semi-double, with spurs about ⅕ longer than the standard of the sepal (pl. 12, and text-fig. 1).

4. *47-98-3* × *47031-1.*—Hybrid Nos. 50-40-1 and 2.

The seed parent was the white *elatum* used in producing the triploids of line 48-27; the pollen parent was also used to produce the triploids of line 50-15. The two individuals of this cross resembled those of 48-27, except that the leaves were more finely dissected, and the flower was the same brilliant cobalt noted in the 50-15 individuals (text-fig. 1).

5. *Derived hexaploid hybrids.*—

Since the fertile strain of *D. Belladonna* apparently originated from spikes whose chromosome numbers had been fortuitously doubled, it was hoped that it might be possible to produce doubling of the chromosomes of the hybrids described above. With this in view the developing rosettes were treated each year for three years with aqueous colchicine in various concentrations for varying lengths of time. In at least one case, doubling of the somatic chromosome number of the spike was achieved, judging not only from morphological features but from greatly increased amounts of "viable" pollen produced (Table I), but the 14 seeds obtained did not germinate.[3] The other method employed, that of repeated selfing

[3]It is not known whether delayed planting or some undetermined genetic factors may have been the cause of the failure to germinate—certainly, one of the chief problems in the growing of *Delphinium* is storage of the seeds. Lots which have germinated well when planted immediately may not germinate at all after six months, even in cold storage.

TABLE I

POLLEN SIZE AND VIABILITY IN SPECIES AND HYBRIDS OF *DELPHINIUM*: LIVING PLANTS.

Plant	% Viable pollen	Pollen diameter in μ	
		Range	Median
Diploids			
D. grandiflorum			
Blue Butterfly	97.0	18.8–37.6	23.5
47031-1	65.0	18.8–28.2	23.5
Tom Thumb	91.0	23.5–37.5	28.2
D. cheilanthum	98.0	23.5–32.9	28.2
Tetraploids			
47-98-3	64.6	23.5–37.5	30.6
Summer Skies	32.0	23.5–37.6	30.6
Triploids			
48-6-1	5.7	28.2–37.5	32.9
48-6-2	7.0	23.5–40.0	32.9
48-27-1	16.0	25.9–40.0	30.6
48-27-3	14.0	23.5–37.6	32.9
48-27-4	6.0	21.2–47.0	35.3
48-27-5	21.0	23.5–42.3	32.9
48-27-6	3.2	23.5–37.6	35.3
48-27-7	9.0	23.5–36.5	32.9
48-27-8	4.0	23.5–42.3	32.9
48-27-10	16.3	21.2–51.7	37.6
48-27-11	5.0	23.5–37.6	30.6
48-27-12	2.7	23.5–47.0	32.9
50-15-1	1.5		
50-15-3	0.0		
50-15-4	2.5		
50-40-2 (untreated)	2.0	21.2–37.6	30.6
50-40-2 (treated)	52.0	25.9–37.6	30.6
Moerheimi	0.5		
Hexaploids			
Smith's *Belladonna*	41.0–95.0	23.5–42.3	32.9
Cliveden Beauty			
-1	68.2	30.6–44.7	37.6
-5	80.5	25.9–37.6	32.9
Lamartine	82.5	23.5–32.9	30.6

of the triploids, proved even less satisfactory, only two inviable seeds being produced from upwards of a thousand individual pollinations made in several seasons. However, pollinations of the triploids by *Belladonna* proved more successful: eventually ten plants, representing five crosses, were obtained, and of these, five plants (representing three crosses) were used in establishing new hexaploid lines, both by selfing and by backcrossing to *Belladonna*. A detailed description of the cytology of these hybrids follows (chapter IV), but it is to be noted that in morphological characters and cytological details they do not deviate from

the *Belladonna* category except in being more variable; and in some cases fertility is already as high as in *Belladonna*.

C. DISCUSSION

Two major points are to be brought out here: First, while it has been demonstrated that there is indeed a resemblance between the Asiatic diploid species *D. cheilanthum* Fisch. *ex* DC. and the hexaploid cultigen, *D. Belladonna*, there are also important differences. The botanical species and its allies are restricted to Siberia, Mongolia, and North China, and to the islands of the Bering Sea and the Yukon, and it has not often been planted in gardens. Moreover, when one comes to compare the two entities, the first impression of similarity is modified by an appreciation of their subtle differences. Thus, the leaf of *D. cheilanthum* may often be incised so that the major divisions are of about the same width and degree of segmentation as in the Belladonnas, yet the latter will invariably have the ultimate divisions more acuminate, the segments often intricate, and the main lateral veins divergent in their departure, features rarely present in *D. cheilanthum*, and certainly never present in combination in that species. The flowers of *D. cheilanthum* are small but always have an extremely conspicuous bee; while the bee of *Belladonna* may be of the same absolute size, it is always smaller in proportion to the size of the flower. Lastly (and it is realized that the botanist will not often have access to the quantity of material necessary to make this distinction), if one has on hand a number of plants of both sorts, it is a relatively simple matter to separate the Belladonnas from *D. cheilanthum*, since the latter holds together by virtue of concordant variation, and the former is less cohesive on account of discordant variation (Anderson, 1951).

The second point brought out in this section is that *Belladonna* types have originated a number of times in the past, and always they have first been noted in gardens. From the evidence, it seems clear that *Hendersoni*, Lamartine, *Moerheimi*, and the others, while not directly related, are quite similar in leaf shape, flowers, branching habit, and prolonged blooming periods. Several of them reproduce by seeds; others have been completely sterile. In no case has the exact origin of the plant been unquestioned. However, all of them have been found to be very much like certain hybrids produced by crossing *Delphinium elatum* and *D. grandiflorum* varieties. In the absence of direct evidence one cannot immediately exclude *D. cheilanthum* as one of the parents, but evidence against such a supposition will be given in the following pages.

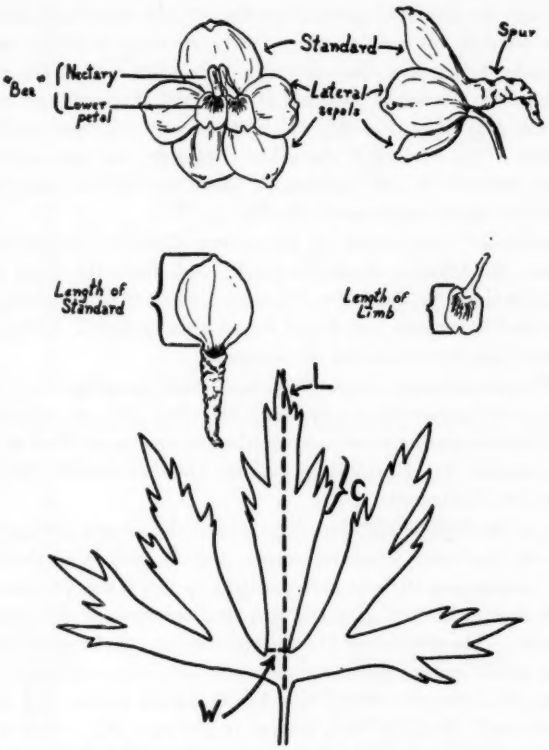
III. Character Association as an Aid in Establishing Relationships

At least since the time of Gmelin, botanists faced with the necessity of classifying species of *Delphinium* have realized the difficulty of finding reliable specific characters. This is the result not so much of lack of genetic differentiation within the genus, as of the presence of numerous characters of a quantitative nature,

whose genetic basis may be modified or simulated by environmental factors. On account of this "inability to use one or two *differentiae* to distinguish species or subspecies," Ewan (1945) has based his treatment of the North American species on "maximum correlation of characters existing in combinations." A species characterized in such terms could be visualized, then, as a plexus of "typical" individuals, possessing the most pronounced correlation of the characters of the species, and a large number of individuals possessing these characters in lesser degree, but with no sharp discontinuities within the group. Such discontinuities, on the other hand, would be expected between species; and populations of hybrid origin might be expected to be largely coherent, but with some segregation if the parental genomes have sufficient segments in common that occasional heterogenetic pairing occurs (chap. IV).

The study of hybrid ancestry in such a group as this would not long ago have been considered a very difficult one from which to arrive at any very definite conclusions. However, the student of variation has been given a valuable tool in the graphic methods developed by Anderson (Anderson, 1948, '51, '52; Anderson and Gage, 1952), which permit the study of complex patterns of variation on the two-dimensional level of the scatter diagram and ideograph. As Stebbins (1952) has recently pointed out, the method of extrapolated correlates involves more than the mere random choice of characters; rather, the choice of a measure is determined by how well it expresses a feature of the plant, and how subject that feature is to environmental variation. While the methods are thus a compromise between pure statistical analysis and subjective intuition, their success in a number of cases indicates their great usefulness.

Before employing these methods in *Delphinium*, it was necessary to study thoroughly within-a-plant variation. Good material for such a study was available in pressed material, and in living plants of several vegetatively propagated individuals, chiefly hybrids of the 48-27 and 50-40 series and Smith's *Belladonna*. Preliminary measurements of a number of characters demonstrated what was already suspected, that only a few features of the leaf could be used. (Leaf variation in *Delphinium* has been the subject of various investigations: Brown, 1944; Lewis, 1947; Ashby, 1948.) By trial and error it was eventually possible to score a number of characters which exhibited low variation even on divisions of a plant grown in different years. In addition to the few leaf characters, those characters most effective for measurement were those of the flowers and inflorescence. (Certain definitive characters, such as internode pattern, mode of branching, etc. could not be employed because of the scanty amount of herbarium material.) With these measurable characters as guides, the three natural species (*D. elatum*, *D. grandiflorum*, and *D. cheilanthum*) and *Belladonna* were studied, and those features which could be used alone or in combinations as differential characters were selected for use in separating the units on a multiple-character basis. The characters used were the following:



Text-fig. 3. Floral and leaf characters used in constructing scatter diagrams.

Leaf.—

Length of median segment/length of *C* (text-fig. 3). Since both measures are about equally dependent on absolute size of leaf, their ratio expresses fairly well the depth of cutting of the segments.

Width of median segment.—

This was found to be the best measure expressing what may be termed the degree of dissection of the segments.

Inflorescence.—

Number of flowers. The absolute number of flowers on the main axis was used.

Density. This was computed as the length of the inflorescence in inches (measured from the attachment of the lowest flower on the main axis) divided by the number of flowers.

Flower.—

Margin of bee. Scored in three grades: bifid, notched, and entire or emarginate.

Length of standard divided by length of limb of the bee (text-fig. 3).

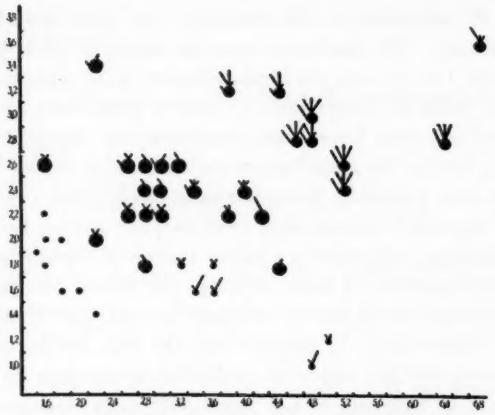
In laying out the scatter diagram (text-fig. 4), the ratios used as ordinate and abscissa were selected because, varying widely among the plants measured and expressed as individual grades, they permit a wide scattering of the points on the diagram. Moreover, the use of measures of one floral character and one leaf character lessens the possibility that they might be merely different manifestations of the same factor. The scoring of the other characters was then adjusted so that each could be expressed in three grades, to which ray lengths and positions were assigned (further details accompany text-fig. 5).

The "population" represented by the scatter diagram consists of herbarium specimens from the Missouri Botanical Garden and from the large collection of cultivated Delphiniums at the Bailey Hortorium of Cornell University. Extreme types such as double varieties and dwarf forms were excluded. All other measurable sheets were included in making the diagrams.

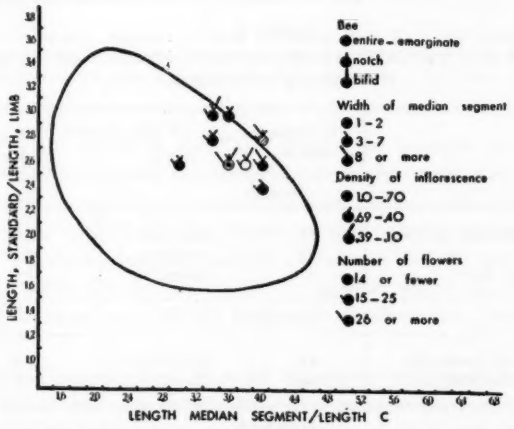
Since pollen measurements made from herbarium specimens were found to be reliable indicators of approximate polyploid level (chap. IV), an additional measure, determined by pollen grain size, is expressed by the size of the dots on the scatter-diagram, the smallest dots representing diploids, the intermediate dots, tetraploids, and the large dots, hexaploids.

A survey of the individuals thus diagrammed shows two distinct entities, *D. grandiflorum* in the lower left-hand corner, and *D. elatum* in the upper right-hand corner. Occupying the area between these species is the *Belladonna* complex, more variable than either but generally intermediate between the diploid and the tetraploid species. The position of *D. cheilanthum* just off the spindle but adjacent to *Belladonna* points out its notorious superficial similarity to *Belladonna*, but its actual physical distinctness is shown first by its diploid nature, and second by its almost "all or none" character with respect to the rays. It is seen to be not an intermediate between *grandiflorum* and *elatum*, but, rather, it possesses some characters in common with *grandiflorum* and some with *elatum*. (The plants of *cheilanthum* scored included two collections of two plants each, as well as two plants growing in the greenhouse at the Missouri Botanical Garden, and so shows more grouping of the dots than would a random selection.)

A graphic analysis of another sort, the internode diagram (text-fig. 6), points out clearly the differences in habit of the entities studied. Both *D. elatum* and *D. cheilanthum* have a relatively large number of nodes before the axis begins to branch; these increase somewhat in length from the highly shortened internodes of the rosette (not illustrated) but do not increase in a regular pattern and are generally not more than 7–8 cm. long. For *D. elatum* this was true not only of the cultigens, but of the wild species as well, where even dwarf alpine plants have a high node number, only the length of the internodes being shortened. In branching pattern these species may also be compared. On the whole (the exception being some garden types which are bred for a diffuse habit) side branches are few and much shorter than the main raceme which they subtend, generally decreasing in length from the lowest to the uppermost. The most evident distinction between



Text-fig. 4. Scatter diagram showing character correlations in *Delphinium grandiflorum* (small dots, rayless), *D. cheilanthum* (small dots, rayed), *D. elatum* (intermediate dots), and *D.* × *Belladonna* Hort. (large dots).



Text-fig. 5. Scatter diagram showing character correlations in members of the 4 triploid populations of this study. Distribution of *D. Belladonna* in outline.

these species, on the basis of habit, is that the inflorescences of *D. elatum* are relatively more highly compressed than those of *D. cheilanthum*.

The habit of *D. grandiflorum* is quite distinctive. Its nodal pattern is typically one of successively increasing internode length from the basal to the sixth rosette, the internodes reaching their maximum length usually by the sixth, and then becoming successively shorter through the inflorescence. While occasional varieties may branch very little, characteristically the plant is much-branched, the branches sometimes being placed at such an angle and being of such a length as to have the superficial appearance of dichotomies. (This is especially true in the closely

related species, *D. tatsienense.*) The branches may again branch in a similar manner (not figured). The maximum internode length in these relatively dwarf plants ranges from 5 to 18 cm., the higher numbers being quite common.

Variability in habit is characteristic of hybrid populations, as Anderson has repeatedly pointed out (see, for example, Anderson and Schregardus, 1944; Anderson and Gage, 1952). In allopolyploids such variability should be small if the variety is of the type termed by Stebbins a true allopolyploid (1947, 1950). If however, it is a segmental allopolyploid, more frequent pairing between members of the different genomes will result in a higher amount of segregation. *Belladonna* does, in fact, vary somewhat in habit, although the general tendency is for these plants to possess a more or less regular internode pattern, with branching common below the main inflorescence. In extreme cases the node number may be low, as in *D. grandiflorum*, and the aspect of pseudodichotomies may be found in the branching pattern; or they may be tall plants with short branches and internode lengths irregular below the inflorescence. On the whole, the direction of variation in this respect tends to be more toward *D. grandiflorum* than toward *D. elatum.*

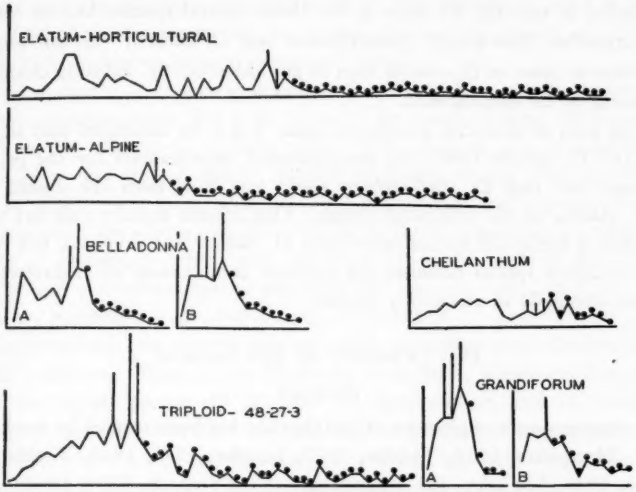
TABLE II

POLLEN SIZE AND VIABILITY IN SPECIES AND HYBRIDS OF *DELPHINIUM*: HERBARIUM SPECIMENS.*

Plant	% Viable pollen	Pollen diameter in μ	
		Range	Median
Diploids			
D. grandiflorum, Vilmorin-Andrieux	98	20.0–25.0	22.5
Blue Butterfly	96	17.5–25.0	22.5
D. cheilanthum, coll. Karo	92	20.0–25.0	20.0
Tetraploids			
D. elatum, Bot. Gard., Cambridge	98	22.5–25.0	25.0
D. elatum, King of the Blues	60	22.5–25.0	25.0
Hexaploids			
D. formosum Hort., N 71860	60	25.0–32.5	30.0
D. formosum Hort., Helms. 17/6/25	25	25.0–32.5	27.5
D. formosum Hort., Dreer, July 1924	50	22.5–32.5	30.0
D. formosum Hort., Fordhook	80	22.5–32.5	30.0
D. Barlowii Hort.†	77	22.5–35.0	30.0
D. Barlowii, Aug. 1†	31	22.5–32.5	30.0
Lamartine, Aug. 20	79	25.0–32.5	30.0

*Specimens listed are in the herbarium of the Bailey Hortorium, Cornell University.

†The confusion as to the identity of *D. Barlowii* has been discussed on page 120. The specimens cited here are morphologically of the *Belladonna* sort.



Text-fig. 6. Internode diagrams to scale of diploid, tetraploid, and hexaploid Delphiniums. Ordinate, length of internode; abscissa, number of internode from rosette. Upright lines represent branches and are drawn to a scale ⅓ that employed for internodes. The black dots represent single flowers.

Text-fig. 5 is a scatter diagram for such of the triploids as were adequately represented by living or herbarium material, and an internode diagram of a typical triploid is shown in text-fig. 6. From the superimposed silhouette of the *Belladonna* distribution (fig. 5) all these plants are seen to be within the limits of that group, or to be intermediate between *D. Belladonna* and *D. elatum*. The same observation is borne out by the internode diagram, which shows the internode pattern of *Belladonna*, but with the high node number more characteristic of *D. elatum*.

Summary.—Through the medium of the scatter diagram it has been demonstrated that *Belladonna* may be visualized as a more-or-less variable group, intermediate between the diploid *D. grandiflorum (vel aff.)* and the tetraploid *D. elatum*, and having as the source of its variation the segregation of characters derived from these species. Further, the experimentally produced hybrids between *D. elatum* and *D. grandiflorum* have been shown to be very similar to *Belladonna*, deviating from it only in characters for which their *D. elatum* parents were extreme. The scatter diagram also amplifies the position of *D. cheilanthum:* it is instantly differentiated from *D. Belladonna* by its diploid constitution, and by constant morphological characters.

The same conclusion is supported by the internode diagrams: there is a greater amount of variability in *D. Belladonna* (extreme types were diagrammed, but are

not included in text-fig. 6) than in the three natural species, but on the whole it is intermediate between *D. grandiflorum* and *D. elatum*. In this respect *D. cheilanthum* is closer to *D. elatum* than to any other entity, differing chiefly in the development of its inflorescence.

On the basis of character association, then, it is to be concluded that *D. grandiflorum* and *D. elatum* fulfill the morphological requirements for the parents of *Belladonna;* but that *D. cheilanthum* could not have been the diploid parent, given *D. elatum* as the tetraploid parent. One cannot thereby rule out the possibility that a tetraploid species other than *D. elatum* was involved, but no other known tetraploid species possesses the required combination of characters, nor is any other tetraploid so commonly grown.

IV. Cytology of Delphinium

HISTORY

The chromosome complement of *Delphinium* has been studied by a number of workers (Hocquette, 1922; Tjebbes, 1927; Langlet, 1927, 1932; Tischler, 1927; Beckman, 1928; Lewitsky, 1931; Lawrence, 1936; Propach, 1939, 1940; Gregory, 1941; Mehlquist *et al,* 1943, and unpublished; Lewis *et al,* 1947; and Lewis and Epling, 1951), and it has now been generally established that the basic complement of the genus consists of one long chromosome with a median centromere, one long chromosome with a sub-median centromere, five medium-length chromosomes with sub-terminal centromeres, and one short chromosome with a sub-terminal centromere. Langlet (1932) reported that satellites occurred in the genus, but his results were not conclusive regarding their number and location. Lewitsky (1931) published some data regarding chromosome differentiation within the genus, and furnished ideograms for a number of species. Noting that in certain instances the four "homologous" chromosomes are not identical, he postulated amphidiploid origin for two tetraploid species, *D. azureum*[4] and *D. elatum*. Moreover, he pointed out that two species belonging to two distinct sections of the genus, *D. cardiopetalum* and *D. Staphisagria,* have distinct types of ideograms from the other species he investigated. More recently, Lewis, Epling, Mehlquist and Wyckoff (1951), reported that the chromosomes of the California species of *Delphinium* (which according to Ewan (1945) include representatives of several of the Old World lines as well as a majority of endemics of uncertain affinities) are morphologically quite similar. They figure a composite ideogram from species included in Ewan's SPICIFORM series, which shows one satellited chromosome (their *E,* which they report is otherwise very close in length to *C, D,* and *F*). That the situation is not so simple as this and that greater possibilities exist for identifying different chromosomes in certain cases have been made clear from the present study in which, apparently for the first time in *Delphinium,* Feulgen and aceto-lacmoid squashes have been employed for somatic material.

[4] *D. azurem* of Lewitsky was probably *D. elatum;* see footnote p. 164.

Numbers of chromosomes published so far in *Delphinium* are listed in the Appendix. Diploid species are by far the most numerous, tetraploids are occasional, and hexaploids are known only in cultivated forms.

Meiotic studies of *Delphinium* have been largely confined to the garden forms, the major exception being the work reported by Lewis, Epling, Mehlquist, and Wyckoff on the California species, where both diploids and tetraploids were analyzed. For the diploid species, metaphase bivalents fall into several easily recognized types, since terminalization regularly occurs and chiasma frequency for a given pair shows little variation, the large chromosomes having usually two chiasmata at metaphase (there may be three or rarely four at diplotene and diakinesis) and the others having regularly one chiasma only, and that in the longer arm (Mehlquist *et al*, 1943; Lewis *et al*, 1951).

In the tetraploids, the type of pairing varies, depending upon the origin of the tetraploid condition. Thus, in the California tetraploids, which are designated as races of the diploid species, *D. Hanseni, D. gypsophilum,* and *D. variegatum,* quadrivalents are formed by about 70 per cent of the long chromosomes with the submedian centromere, and by about 45 per cent of the long chromosomes with the subterminal centromere. (Likelihood of multivalent formation by the other chromosomes is precluded by their known low chiasma frequency.) Anaphase separation is regular, and the plants are fully fertile. However, it was demonstrated that the chromosomes are not completely homologous, since anaphase bridges indicative of inversions were common.

Of other tetraploids studied, Lawrence (1936) recorded one to four univalents and an undetermined number of multivalents in *Delphinium Ruysii,* a garden hybrid possessing one *D. elatum* (n = 16) and two *D. nudicaule* (n = 8) genomes. A similar condition was found to exist in a group of tetraploid hybrids produced by Mehlquist (unpublished) from crossing *D. elatum* with artificially doubled *D. cardinale,* in which meiotic pairing was found to be primarily by bivalents and univalents, although segregation in succeeding generations indicated that some multivalent pairing occasionally occurred.

Particularly interesting in so far as this study is concerned are the varieties bred by K. Foerster of Bornim, Germany, and studied by Propach (1939, 1940). According to Propach, Foerster produced his hybrids by intercrossing *D. Belladonna* varieties and *D. grandiflorum* var. *chinensis,* obtaining in the first generation fully fertile tetraploids. Later, some of these hybrids were again crossed with *D. grandiflorum* to form sterile triploids (Appendix). Unfortunately, full cytological details were not given. Propach interpreted his results as indicating that there is little genomic differentiation in *Delphinium* and that autopolyploidy is involved.[5]

[5]However, Foerster (1929) does not give details about the parentage of his varieties in all cases, and of those which he discusses, some he terms *elatum* types and some *elatum* × *grandiflorum* var. *chinense* hybrids. Further, the accompanying plates confirm his statements; therefore a thorough cytological study of these forms is desirable before Propach's conclusions can be accepted.

The first object of this study was to discover whether any morphological differentiation of the chromosomes could be made among species of *Delphinium*, so that, if possible, the component genomes of the polyploid species might be identified. The second phase of the cytological work has dealt with the meiotic behavior of the chromosomes in the species and hybrids. Data obtained from chromosome studies have been supplemented by pollen studies which, to some extent, serve to indicate the degree of fertility of a plant; and pollen measurements have been used, especially of herbarium specimens, to give information (which could not be obtained by other means) on the probable polyploid level of these plants.

METHODS

1. *Somatic Tissues—Chromosomes:*

Although the paraffin method has been the one used by previous workers, it was seldom employed here. This was not only on account of the length of time required to prepare the mounts, but also because root tips from sectioned material did not show the structural features evident in acetic squashes, nor could counts of chromosome number be made so readily. For squash techniques, it was necessary to adapt the method to the particular requirements of the material. Pre-treatment with a spindle inhibitor was found to be essential since the chromosomes of metaphase plates were otherwise obtained in face-view only with the greatest difficulty; further, aceto-carmine did not give the degree of differentiation obtained with aceto-lacmoid. The schedule follows:

a. Actively growing root-tips were removed and treated with a saturated solution of paradichlorobenzene (Meyer, 1945) for 3 to 4 hours.

b. Tips were transferred to 7:3 acetic alcohol (Darlington & La Cour, 1947) for 1 to 5 days. Preparations from material preserved longer than this are not clear enough for studies of details of chromosome morphology, but are adequate for counts.

c. Tips were hydrolyzed in a mixture of approximately 2 drops 0.1 normal HCl and 5–6 drops acetic-lacmoid stain (Darlington & La Cour, 1947), heating on a glass until vapor could be seen, and then letting the tips remain in the mixture for 10 to 20 minutes, or until they became soft. (Sometimes it was necessary to increase the proportion of HCl in the staining mixture in order to soften the tips sufficiently, but generally as little acid as possible was used since an excess decreases staining.)

d. Root tips were rinsed in 45 per cent acetic acid for 5 minutes to about an hour.

e. The deeply stained portion of a tip was transferred to a clean slide, and stain and cover-glass were added. The mount was heated and squashed and then sealed. After the cells were dispersed by gentle tapping, considerable pressure could be applied in order to spread out their contents.

The preparations will keep for about a week if stored in a cool place, but they are best within a few hours after being made.

2. *Somatic Tissues—Nucleoli:*

The Feulgen-fast green squash technique (Darlington & La Cour, 1947) was used. Hydrolysis time was about 20 to 40 minutes.

3. *Meiotic Chromosomes:*

The exact method used depended upon the age and condition of the material. In general, the following schedule was employed:

a. Anthers were killed and fixed in acetic alcohol for several hours to a week or more. (Best results were obtained if mounts were made in about one to four days.)

b. A whole anther was transferred to a slide, flattened with the needle, and stained.

1. Fresh material: acetic lacmoid gave the best results.

2. Older material: a mixture of aceto-lacmoid and aceto-carmine was employed, the relative amount of carmine being increased with increasing age of the material.

3. If the material was not stored for more than two weeks, it could be transferred to 70 per cent ethanol, and thereafter stained with carmine, in which case mordanting was found to be necessary.

c. A cover slip was added and the slide was squashed gently and sealed. After the slide had been sealed it could be heated and again squashed if necessary.

4. *Pollen Studies:*

Preparations were made with either aceto-carmine or acid fuchsin, at least three slides being made for each plant of which the pollen was available. The anthers were taken on different days and from different flowers so that the effect of environmental variation could be observed. A total of 200 pollen grains was counted on each slide, only the deeply staining, normally shaped grains being considered "viable." Where possible, 100 good grains of each individual were measured, but in the triploids the number is understandably considerably less.

Pollen preparations from herbarium specimens were made employing the fast-green glycerine jelly method of Wodehouse (1935).

5. *Illustrations:*

Camera-lucida drawings were made with a Spencer Camera Lucida on a Spencer microscope with 15 × ocular and 95 × N.A. 1.40 apochromatic oil-immersion objective, giving a magnification of 2180 × at table height. Reductions are given with each figure. The photomicrographs were taken with a 1 × Bausch & Lomb fixed bellows camera; magnifications accompany the plates and text-figures.

DETERMINATION OF THE LEVEL OF PLOIDY

While the determination of polyploid level in the living plants was always made by chromosome counts from root-tip preparations, the impossibility of applying direct methods to plants represented only by herbarium material made necessary the use of the indirect method of pollen measurement. In studying the percentage of "viable" pollen produced by hybrid individuals, it had previously

been noted that diameter of the pollen grain was a good indicator of the polyploid level of the plant (Table I). For the plants measured there was good separation of diploids and tetraploids on this basis. The hexaploids and triploids generally produced the largest pollen, although there was some overlapping between these and *D. elatum*. It is to be noted that pollen production by the triploids is very low (except in the colchicine-treated spike of 50-40-2, which is presumed to have been doubled); the similarity in size of their few pollen grains to that of the hexaploids is an indication that the pollen from these plants is unreduced, and hence triploid.

For pollen grains of the herbarium specimens, size of pollen grain was again found to be a differential character for the polyploid level, although the actual sizes obtained were somewhat smaller in all classes, as might be expected on the basis of the difference in the suspending medium of the stain and from long drying of the material (Table II).

CYTOLOGY OF NATURAL SPECIES, *DELPHINIUM BELLADONNA*, AND THE TRIPLOIDS

Morphology of the Somatic Chromosomes.—

In view of the general similarities in size of the chromosomes already noted as characteristic of the genus, ideograms are presented here for two species only: *D. grandiflorum* var. *chinensis* and *D. cheilanthum*. The *A* and *B* chromosomes of these species probably are to be compared with similarly lettered chromosomes in the ideograms of Lewitsky (1931) and Lewis *et al* (1951), but because of the similar sizes of the smaller chromosomes it is not to be assumed that these are comparable to similarly lettered chromosomes in the other ideograms.

The major distinguishing features of the genomes figured here (pl. 13) have been the satellite-bearing chromosomes. The presence of nucleolar-organizing satellited chromosomes in the complement of many plants has been often noted since the classic papers of Heitz (1931), Navashin (1934), and McClintock (1934). Later, the discovery of polyploid species in which the satellite number was comparably increased led certain workers to assume that often, if not always, apparently diploid species which possessed several satellites in the gametic complements are actually of polyploid derivation. This was the view held by Gates, who published a comprehensive review on this subject in 1942. However, since many polyploids never have more than two satellites, and since, on the other hand, in such plants as *Leontodon leysseri* three of the four chromosomes of the haploid complement bear satellites (Elliot, 1950), inferences as to polyploid level based on satellite or nucleolar number alone must be regarded as unsound.

Another problem related to the existence of satellites must be considered in order to appreciate the variations in satellite number observed in the *Delphinium* hybrids, and that is differential amphiplasty. This phenomenon was first noted by Navashin (1927, quoted by him in 1934), who applied the term to the apparent loss of satellites which sometimes occurs in hybrids. The following year, McClintock, in her paper on the nucleolar organizing chromosome of *Zea Mays*,

discussed in detail Navashin's work, interpreting the loss of satellites in hybrid forms as being due to the inability of the chromosome to "organize" a nucleolus in the presence of another more "active" chromosome. Amphiplasty has recently been reported in the genus *Leontodon* (Elliot, 1950), and had been occasionally reported in other genera (Meurman and Therman, 1939; Levan, 1937).

While our present understanding of differential amphiplasty is by no means perfect, the cases cited above seem to show that under certain conditions such as obtain in some hybrid cells, the apparent morphology of nucleolar organizing chromosomes may be modified. Since the presence of a satellite at metaphase is usually directly related to the formation of a nucleolus in that region in the preceding telophase, then the causative factor is apparently related to nucleolar metabolism. Nevertheless, the actual physiological differences between individual nucleolar "organizers," which are the essence of the problem, are not known at all, and it is therefore the morphological aspect of the phenomenon which concerns us here.

Diploids.—In pl. 13 is given the ideogram of *D. grandiflorum* L. var. *chinensis* Fisch. hort. var. Blue Butterfly, pollen parent of the 48-27 and 48-6 series of triploids. The actual length of metaphase chromosomes ranges from 3.1 to 10.1 μ. (These measurements are based on chromosomes not artificially contracted by PDB, although the chromosomes measured were subjected to minimum treatment in order that the spindle would not interfere with their being well-flattened.) Of the shorter, subterminally constricted chromosomes, chromosome *H* is readily identified by its length as well as by the satellite; of the rest, chromosome *C* may be identified by its satellite and sometimes by the secondary constriction of the long arm. Chromosomes *D* through *G* are individually distinguishable only with difficulty; the lengths of their short arms, on the whole, were found to be more diagnostic than the long arms, which may be variously extended, being slower to complete their coiling cycle than the short arms.

A difference in the activity of the satellites was noted here. While usually both *C*'s were satellited, no cells were ever observed in which at least one *C* did not bear a satellite; the satellite of the *H* chromosome, on the other hand, was commonly present in unicate, and sometimes was even missing altogether. This was generally true for all plants of *D. grandiflorum* and was statistically determined for two individuals (Table III).[6]

Related plants, including 47031-1 from the Royal Botanic Gardens at Kew, *D. grandiflorum* L. var. *chinense* Fisch. from Basel, and numerous plants of horticultural varieties such as Tom Thumb and White Butterfly were examined and found to have a similarly differentiated complement (pl. 13). 47031-1 was found to possess a telocentric fragment, about the length of the long arm of the *H*

[6]In the course of numerous observations, in one plant of this species a third satellite was noted on one of the intermediate chromosomes, but as it was not present in any other case it has been omitted from the ideogram.

chromosome. Though the numbers of fragments present in different cells of an individual have been found to vary somewhat, the fragment is commonly transmitted through the gametes, being found in plants three and four generations removed from 47031-1. Unfortunately, the original plant and the fragment-bearing triploids were lost before pairing affinities of the fragment could be determined, and there are sufficient irregularities in the descendant hexaploids to make its identification in PMC's doubtful.

Plants of *D. tatsienense* Franch., a species closely related to *D. grandiflorum* L., were found to possess a genome similarly differentiated except that in the individuals surveyed the satellite is as often developed on the *H* chromosome as on the *C* chromosome (see 51-311-9, Table III).

D. cheilanthum.—By contrast with *D. grandiflorum, D. cheilanthum* bears its satellites on the *A* and *C* chromosomes, that on the *A* being not only larger but also the more "active" of the two (Table III, 51-307-6 and 51-307-1). So far as can be ascertained, the chromosomes of the two species are otherwise similar, except that the satellite-bearing arm of *A* is slightly longer here than in *D. grandiflorum.*

TABLE III

SATELLITE EXPRESSION IN *DELPHINIUM* SPECIES AND HYBRIDS

Plant	Fraction of chromosomes bearing satellite*			Number of cells	Theoretical satellite number	Actual average satellite number
	C	H	A			
Diploids						
grandiflorum						
51-312-6	0.94	0.48	—	100	2:2:0	1.8:1.0:0
51-315-6	0.91	0.62	—	100	2:2:0	1.8:1.2:0
tatsienense						
51-311-9	0.85	0.80	—	100	2:2:0	1.7:1.6:0
cheilanthum						
51-307-6	0.47	—	0.95	100	2:0:2	1.0:0:1.9
51-307-1	0.49	—	0.98	100	2:0:2	1.0:0:1.9
Tetraploids						
D. elatum						
51-318-2	0.56	0.12	0.83	21	4:2:2	2.2:0.25:1.6
51-318-4	0.50	0.07	0.92	71	4:2:2	2.0:0.15:1.8
Triploids						
48-27-3	0.61	0.33	0.05	100	3:2:1	1.8:0.67:0.05
50-15-3	0.52	0.34	0.63	100	3:2:1	1.5:0.68:0.63
Hexaploids						
Smith's *Belladonna*	0.63	0.10	0.84	25	6:4:2	3.6:0.4:1.6
51-232-4	0.45	0.25	0.13	60	6:4:2	2.7:1.0:0.3

* Fraction is computed on the basis of the actual observed maximum number of satellites for that chromosome.

Other diploids.—A third situation with respect to satellite number and position was found in *D. cardinale* (pl. 13) and *D. nudicaule* from California, and a fourth in *D. Zalil* Aitch. and Hemsl. (native to Persia and Turkestan) and *D. sulphureum* Boiss. and Hausskn. (from north Syria). In the California species the satellite number is 3, and the satellites occur on the *H* and on two pairs of intermediate chromosomes, one of which may or may not correspond to *C*, the lengths of the chromosomes in these species being not exactly comparable to those of *D. cheilanthum* and *D. grandiflorum*. The third satellite is on the second shortest chromosome. Despite the high potential satellite number, the low number of nucleoli usually present at telophase and interphase (generally no more than 4) indicates that all are rarely active in a particular mitotic cycle. In *D. Zalil* and *D. sulphureum* satellites occur on *A* and on one of the intermediate chromosomes. However, the genome differs from that of *D. cheilanthum* in the arm lengths of the intermediate chromosomes, so that direct comparisons cannot be made.

In studying satellite development in the above diploid species a situation was noted which has apparently not been described before, namely, that even within old diploid species differential "activity" of satellited chromosomes may be common. With this in mind further variations in satellite development which are found in polyploid species may not be so unexpected. In order to avoid ambiguity here, I shall use the term "differential activity" to apply to the differences in satellite development such as characterize diploid species, and "amphiplasty" to refer to any pronounced alteration in differential activity which follows hybridization. Actually, however, it is not to be assumed on such scanty visual evidence that any physiological distinction is being made.

Tetraploids: D. elatum.—In *D. elatum*, the only tetraploid species observed, distinctions among the chromosomes are again difficult to make. There are 2 pairs of long, medianly constricted *A* chromosomes, 2 pairs of long, sub-medianly constricted *B* chromosomes, 10 pairs of intermediate chromosomes with subterminal constrictions, and two pairs of short chromosomes with subterminal constrictions. Amphiplasty obscures the satellite situation, the more active *A* and *D* satellites usually being the only ones present (Table III), but a study of a large number of cells, both in the species (accessions from Göteborg Botanic Garden, and the Royal Botanic Gardens at Kew) and of horticultural variants, indicates the presence of satellites on 1 *A*, 2 *C*'s and 1 *H* of the haploid complement. Although the number of satellites in the tetraploids parental to the triploids could not be determined statistically, camera-lucida drawings of the complements of 47-98-3 and Summer Skies indicate that these plants were typical in this respect (pl. 14). As in *D. cheilanthum*, the satellited *A* chromosome stands out from its counterpart in the other genome by virtue of its longer satellited arm. Lewitsky (1931) noted this difference in length, but did not observe the satellite.

The nature of the chromosome differentiation in *D. elatum* is thus strongly suggestive of an allopolyploid origin by hybridization and subsequent doubling of the chromosome number of diploid forms whose chromosome complements were of

the types represented in present-day species *D. grandiflorum* and *D. cheilanthum*. That the chromosomes designated at *C* are truly comparable in the two genomes and are not different members of the medium-sized group is corroborated by the fact that both possess a secondary constriction of the longer arm.

Aneuploids are occasionally found, even among the plants from the botanic gardens. However, they do not possess the abnormal characteristics which ordinarily distinguish aneuploids on the diploid level, and fertility, as judged by amount of seed produced, is apparently not greatly impaired.

Triploids.—All plants of the four groups of triploid hybrids were examined and found to be essentially similar in so far as the morphology of the chromosomes is concerned (pl. 14). The maximum satellite number in each is 6: 1 *A*, 3 *C*'s, and 2 *H*'s, as would be expected on the basis of the generally regular segregation of the parents. The precise situation as to satellite development has been thoroughly worked out only for two individuals, 48-27-3 and 50-15-3, most of the other plants having died before this part of the study was undertaken. An interesting case is 48-27-3, in which the satellited *A* chromosome, so active in *D. elatum*, is rarely developed. (Study of camera-lucida drawings of other plants of this line and of the very similar 48-6 line indicates that this is generally true of both groups.) However, in 50-15-3, the other triploid analyzed, the *A* satellite was observed in more than 80 per cent of the cells examined. Thus, in crosses of similar parentage, amphiplasty has been demonstrated in one case, but did not occur in another.

With regard to the centric fragment of their pollen parent 47031-1, triploids 50-15-1 and 50-15-4 were found to possess the fragment in most cells; 50-15-3, 50-40-1, and 50-40-2 lack the fragment.

Hexaploids.—The tendency already noted for partial suppression of the potential satellite number was especially evident in the hexaploids, of which Smith's *Belladonna*,[7] Cliveden Beauty, Bellamosum, and Lamartine were observed in some detail, as well as in the derived hexaploids which are to be considered in chap. V. In most cases, cumulative records on these plants indicated a possible satellite number of 2 *A*'s, 6 *C*'s, and 4 *H*'s of the diploid complement. However, the normal satellite number in individual cells is often only half this number (pl. 15).

When interplant variation in degree and type of amphiplasty was studied Smith's *Belladonna* was found to possess very active *A* SATs, but among its progeny obtained by selfing, all degrees of activity were found; this was also true of the F_1 obtained by crossing this plant with Bellamosum. At the other extreme are certain individuals of Bellamosum, in which the satellited *A* can rarely be distinguished (Table III).

Meiosis and Fertility.—

Meiotic studies have been made of the triploid hybrids and their parents, where these have been available, as well as of *Belladonna* varieties, in an effort to compare

[7] The plant termed "Smith's *Belladonna*" throughout this study is a selection from the horticultural variety "Cliveden Beauty."

TABLE IV. MEIOSIS OF THE TETRAPLOIDS

	Plant		47-98-3	Summer Skies
Metaphase configurations	16 II		18	11
	15 II, 2 I		2	7
	14 II, 4 I		0	5
	13 II, 6 I		0	0
	12 II, 8 I		0	0
	11 II, 10 I		0	1
	Number of cells		20	24
First Anaphase	Number cells structurally abnormal		88	11
	Number cells structurally normal		112	124
	Total		200	135
	% abnormal		44.0	11.3
Second Anaphase	Number cells structurally abnormal		4	3
	Number cells structurally normal		16	31
	Total		20	35
	% abnormal		20.0	10.3

TABLE V. METAPHASE PAIRING IN THE TRIPLOIDS

Plant	8 II, 8 I	7 II, 10 I	6 II, 12 I	5 II, 14 I	4 II, 16 I	3 II, 18 I	2 II, 20 I	1 II, 22 I	24 I	1 III, 7 II, 7 I	1 III, 6 II, 9 I	1 III, 5 II, 11 I	1 III, 4 II, 13 I	1 III, 3 II, 15 I	1 III, 2 II, 17 I	1 III, 1 II, 19 I	1 III, 21 I	Total cells
48-27-2	20	2	7	7	5	2	6	2			2	1	2					37
48-27-3	20	14	9	9	8	2	1			3	4	2	2	1				74
48-27-5	2	18	20	18	6	1				3	2	1	1					92
48-27-6		3	5	7	1	5	1				1	2	4					30
48-27-12		1	3	5	6	2	2	2				3	1					25
48-6-1		2			3	1	1			1								5
8-6-3			1	1		1												6
50-15-1	1	7	7	6	2	5		1					2	2	1			19
50-15-3	30	3	3	1	2	3												47
50-15-4				1			1	1										15

chromosome homologies in the triploids and *Belladonna*. Early prophases are usually difficult to stain by squash methods, and while fair preparations can be made by paraffin sections, using gentian violet stain, the high number of chromosomes present makes prophases generally of less use than later stages, which can readily be stained by conventional squash methods. For the most part, configurations at diakinesis and metaphase were analyzed, and anaphase I and II were scored for structural abnormalities. However, counts of chromosome segregation were not made, since the frequent occurrence of aneuploids in all polyploid populations is sufficient evidence that hyperploid and hypoploid gametes are produced.

The approximate percentage of "viable" pollen produced by certain key plants is given in Table I. However, since samples from the same plant taken on different days may show a wide range of viability, the values given can scarcely be considered absolute indications of fertility. Moreover, apparently good grains may not survive until the pollen tube has reached the ovule, not only on account of some deficiency of the grain, but also, perhaps, because of incompatibility with the stylar tissue. Certainly, the particular environmental conditions prevailing at the time of pollen formation and shedding are not the least important factor in the production of functional pollen and its further development. It has repeatedly happened that a plant which produced a large amount of well-filled, staining pollen grains and set a high percentage of viable seeds at one time, produced little pollen and set few seeds at another time, or again, produced apparently good pollen but set no seed. The immediate cause of impaired fertility of this sort is often a prolonged hot spell, but other factors may have a similar effect.

Diploids.—Blue Butterfly is usually quite regular in meiosis. In almost every one of numerous cells examined at diakinesis and MI, pairing was in 8 bivalents (pl. 15). Chiasma frequencies ranged from 2 to 3 for chromosomes *A* and *B*, to 1 or occasionally 2 for the others. Anaphase separation is quite regular, bridges occurring in less than 1.0 per cent of the cells examined. A regular second division is followed by the simultaneous cleavage of the pollen mother cell into tetrads.

Unfortunately, metaphase pairing of 47031-1 was not observed during the first year and the plant was subsequently lost. In anaphase I, however, laggards (probably the fragment) were noted in 9 per cent of the cells, and bridges in 3 per cent of the cells. The amount of "viable" pollen was about 65 per cent. The presence of the fragment in two of the five triploid offspring of this plant is satisfactory indication that pollen fertility was not prevented by the possession of the fragment. However, whether the failure of the plant to set any seed when self- or cross-pollinated may indicate some deleterious effect of the fragment in the ovule cannot now be shown. This case thus appears to be quite different from that of the centric fragment studied by Rhoades in *Zea* (1940), where transmission of the fragment was largely through the egg, fragment-bearing pollen grains usually not competing successfully with normal pollen grains.

Tetraploids.—Meiosis of Summer Skies is not entirely regular, the occurrence of 2 to 4 univalents at metaphase I being rather frequent. Further evidence of

structural hybridity is given by anaphase I and second-division configurations, bridges, fragments, and lagging chromosomes being present in 11.3 per cent of the A I and 23.3 per cent of the A II cells examined (Table IV). Pollen viability appeared to be rather low (Table I), but that the plant is highly fertile has been indicated by the amount of seed produced.

47-98-3 exhibited fairly regular pairing; only two of the twenty diakinesis and MI plates showed each 2 univalents. However, a higher proportion of the large chromosomes had reduced chiasma frequency, with sometimes only 1 chiasma per bivalent. Further evidence of chromosomal hybridity is seen in the rather high number of cells at anaphase I which showed visible abnormalities (44.0 per cent). Abnormalities of the second division were less frequent, being present in only four of twenty cells examined. Pollen viability was about 65 per cent.

47-2-3, the tetraploid parent of the 48-6 group, was not available for study.

Triploids.—Representatives of the several crosses have been analyzed. Since the number of PMC's examined in each case have not been large enough to permit separate discussion, the data have been somewhat grouped.

48-27-: Numbers 2, 3, 5, 6, and 12 have been studied (Tables V and VI, pl. 15). Metaphase pairing is largely in bivalents and univalents, only 34 trivalents having been found in the 258 cells analyzed. Usually, the long chromosomes (*A* and *B*) were involved in the trivalent configurations, but trivalents formed by chromosomes of intermediate size were found at least twice. The low number of trivalents involving the intermediate chromosomes may be due in part to their observed low-chiasma frequency, but also to the presence of differentiated segments. The amount of even the *A* and *B* chromosomes present in trivalents is only 7.2 per cent.

In two individuals (48-27-3 and 48-27-5) bivalent formation is near the maximum number expected if normal chiasma frequencies prevail—that is, if those chromosomes which pair form the normal number of chiasmata. However, whether such pairing is ordinarily between the 8 chromosomes contributed by *D. grandiflorum* and 8 chromosomes of *D. elatum,* or whether pairing is primarily within the *elatum* complement only can not be determined precisely. The above-mentioned occurrence of occasional trivalents does indicate that some mixture of the two sorts prevails. That intragenomic pairing may occur in *D. elatum* is already known from the work of Lawrence (1936) and Mehlquist (unpublished); but the morphological similarity of one *D. elatum* genome to that of *D. grandiflorum* is equally strong indication that pairing between these chromosomes cannot be discounted.

Despite the rather high proportion of bivalents which may be formed in certain individuals, the frequency of univalents, which may sometimes number as many as 22, is indicative of structural differentiation of the chromosomes. This is further substantiated by the high percentage of structural abnormalities observed at anaphases I and II. At least one bridge-fragment was observed, on the average, in about 50 per cent of the cells examined, both at A I and at A II. Such config-

TABLE VI
MEIOTIC ANAPHASES OF THE TRIPLOIDS

Plant	Anaphase I						Anaphase II					
	Bridges & fragments	Laggards	Both	Structurally normal	Total	Per cent abnormal	Bridges & fragments	Laggards	Both	Structurally normal	Total	Per cent abnormal
48-27-2	16	17	10	21	64	67.2	7	1	5	17	30	43.3
48-27-3	41	61	14	92	208	55.8	16	15	11	25	67	62.7
48-27-5	29	33	12	33	107	69.2	12	7	5	35	59	40.7
48-27-6	10	21	9	23	63	63.0	—	—	—	—	—	—
48-27-12	44	25	16	39	124	68.4	—	—	—	—	—	—
48-6-1	36	10	7	29	82	64.7	3	1	3	7	14	50.0
48-6-3	13	10	6	25	54	53.7	13	11	5	10	39	74.3
50-15-1	21	8	4	34	67	50.9	10	6	7	7	30	76.6
50-15-3	14	1	4	28	47	40.5	11	4	4	22	41	46.3
50-15-4	19	2	4	37	62	40.3	—	—	—	—	—	—

urations have been shown by others to be caused by crossing-over within inversions, by crossing-over involving certain types of duplication (McClintock, 1941) or, as suggested by Emsweller and Jones (1938), by pairing between chromosomes whose insertions are not opposite.

The number and behavior of the lagging chromosomes are of interest. The average number of laggards was less than one per cell in A I, and even lower in A II. As a result, except for the numerical imbalance of most of the gametes formed by these plants in natural consequence of their triploid constitution, the loss of univalent chromosomes, which is often characteristic of such plants, was not pronounced. This point will be considered further in the treatment of the hexaploids.

The number of microspores per tetrad is variable, 2 and 3 being the more common variants, but a fifth micrograin is occasionally formed. Micronuclei are extremely common, but are usually included with one of the other nuclei within a common wall.

The amount of apparently good pollen has been found to be quite small, and that which is formed is within the range of pollen size of the hexaploids, suggesting that such pollen is actually unreduced (Table I).

48-6-: Numbers 1 and 3 of this line were briefly analyzed. There was apparently a greater tendency to bivalent formation in 48-6-1, 7 II having been noted in several cases, while 2–6 II were found in 48-6-3. One trivalent was noted in 48-6-1. In anaphase I and anaphase II somewhat higher frequencies of abnormalities were noted in 48-6-1 than in 48-6-3.

Viable (unreduced) pollen grains were formed in 2.8 per cent of cases in 48-6-3 and 5.7 per cent in 48-6-1 (pl. 15).

50-15-: Numbers 1 and 4 have been examined and seem to differ somewhat in pairing relationships. Single trivalents involving the large chromosomes occurred in 5 of 18 figures in 50-15-1, whereas no trivalents were noted in the 15 cells of 50-15-4 analyzed. Structural abnormalities at A I were present in about 40 per cent of the cells of each, and there were many irregularities at A II. Pollen viability was determined at 1.5 per cent and 2.5 per cent for numbers 1 and 4 respectively.

50-40-: A survey of meiosis in 50-40-2 indicated that pairing was usually in 5 to 7 bivalents, with an occasional trivalent. Reduced chiasma frequency was evident in the *A* and *B* chromosomes, and abnormalities of later stages were frequent.

Moerheimi was lost early in the study, but preliminary observations indicated that meiosis was comparable to the three hybrid groups. Pollen viability was extremely low, less than 0.5 per cent unreduced pollen grains having been found.

Hexaploids.—Belladonna: Lawrence (1936) has reported that meiosis in this form is largely regular. In Cliveden Beauty, a light-blue *Belladonna* variety, 2 to 4 univalents (of small or intermediate chromosomes) were noted in 10 out of 16 MI cells, but the chiasma frequency of the *A* and *B* chromosomes was only slightly reduced. At anaphase I structural abnormalities were visible in 12.3 per cent of the cells. Anaphase II was quite regular, only 7 of 121 PMC's being visibly abnormal. Individuals of this variety were found to have from 63.2 to 80.5 per cent of good pollen.

Preparations of Smith's *Belladonna* showed somewhat less regular pairing at metaphase, with up to 8 univalents and the *A* and *B* chromosomes often with but one chiasma per pair. The actual amount of pairing was somewhat higher, however, for in diakinesis univalents were uncommon and the large chromosomes had mostly two or three chiasmata in each bivalent (Table VII, pl. 15).

Table VII gives some indication of the irregularities which are found in *D. Belladonna* varieties, although the plants cited by no means represent a random sample. A certain number of univalents are almost always present, but they assort at random and do not commonly lag at the plate. Multivalents are rare, but were noted in 52-325-11 (Smith's *Belladonna* × self), where both the *A* chromosomes and intermediate chromosomes were observed in such configurations. However, although one *A* chromosome was lacking from this plant, the monosome was unusually unpaired.

The consequences of such irregularities as have been observed in *Belladonna* are indicated by somatic counts in various populations involving this variety. Text-fig. 7 compares the range in chromosome numbers of randomly selected progeny of various crosses. Thus, in 51-224 (Smith's *Belladonna* × Bellamosum, a dark blue *Belladonna* segregate) 8 of the 15 plants in the sample possessed 48 chromosomes, and in 52-311, produced by selfing a 48-chromosome individual of

TABLE VII
MEIOSIS IN BELLADONNA TYPES

Plant	Metaphase I						Anaphase I				Anaphase II			
	Chromosome number	Number of cells	Number bivalents per cell—range	Total number multivalents	Number multi. involving intermediate c-somes	Median number bivalents	Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells	Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells
Smith's Belladonna*	48	55	24–20	0	0	23	12	2	2	33.3	Mostly regular			
Cliveden Beauty-5	48	15	24–22	0	0	23	81	3	3	7.4	121	4	3	
52-325-11	47 (5A)	32	23–19	4	2	22	48	3	9	25.0	—	—	—	
51-224-16	48	21	24–22	0	0	23	29	4	7	35.9	14	1	0	
51-232-47	49	45	24–19	0	0	23	100	9	34	43.0	65	4	19	
Lamartine	48	46	24–21	0	0	23	67	6	4	14.9	104	7	6	

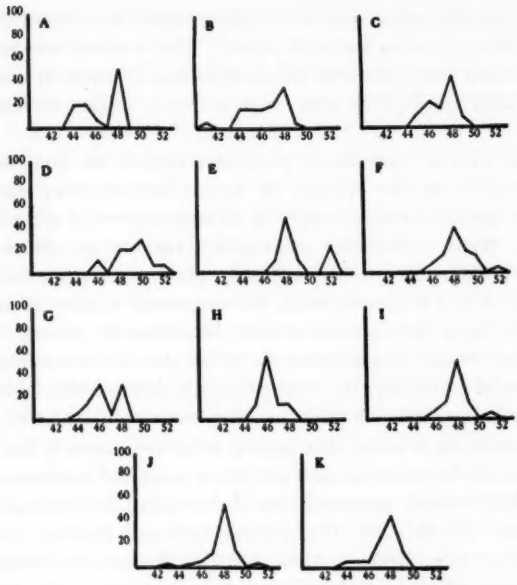
*Of 21 late prophases observed, 17 showed 24 II, and 3 had each 23 II and 2 I. One cell had 6 univalents.

this population, chromosome numbers of 25 plants ranged from 41 to 49, only 7 individuals having the "normal" number. Again, among 25 individuals of cross 51-232 (Bellamosum × self) chromosome numbers ranged from 45 to 49, 11 plants having the 48 chromosomes expected. In a sample of 10 plants obtained by selfing Smith's *Belladonna* (not figured), numbers ranged from 46 to 48. In most of the above cases the additional or missing chromosomes were of the smaller classes, but one plant with 48 chromosomes (51-232-1) lacked an *A;* and 51-224-13, with 45 chromosomes, lacked a *B.* None of the aneuploids were visibly abnormal, and such observations of pollen viability as were made revealed no obvious correlation between chromosome number and pollen viability. Evidently, like many other polyploids, *D. Belladonna* can withstand the loss of a certain amount of genetic material without suffering the consequent weaknesses and abnormal development common when such losses occur at the diploid level.

Discussion and Summary.—

The cytological information given above bears on the problem of the identity of the genomes in *D. Belladonna* both from the standpoint of chromosomal morphology and of pairing homologies of the chromosomes in meiosis.

The somatic studies have made clear that the aspect of the chromosomal complement of *D. Belladonna* is just what might be expected if it had been produced by doubling the chromosome number of such a triploid as those produced here. The amphiplasty of the satellite of the *A* chromosome in different plants of *Belladonna* was also found in different triploids. That this differential activity is



Text-fig. 7. Frequency distributions of chromosome numbers in populations of *D. Belladonna* and of the derived hexaploids. Ordinates represent per cent of population; abscissa, number of chromosomes.

A—51-224	D—51-216	G—51-219	J—51-222
B—52-311	E—51-217	H—51-220	K—51-223
C—51-232	F—51-218	I—51-221	

not equivalent to morphological loss of the satellite was made evident by analyses of certain plants in which the rare occurrence of the satellite proved that its usual absence does not represent permanent loss. This condition is thus different from the actual morphological differences in satellite disposition between the chromosomes of the two diploids *D. grandiflorum* and *D. cheilanthum*.

Recognition of this difference is important for the interpretation of the satellite pattern in *D. elatum*, the various triploids, and *D. Belladonna*. Thus, *D. elatum* might be a derivative of two diploid species whose genomes were differentiated along the lines of present-day *D. grandiflorum* and *D. cheilanthum*. And, given *D. elatum* as the tetraploid parent of *D. Belladonna*, *D. grandiflorum* might be the diploid parent; but *D. cheilanthum* could not have been, unless drastic morphological alterations of the chromosomes have ensued since the time of origin of *Belladonna*. If the alternative supposition is made, that *D. cheilanthum* was the diploid parent of *Belladonna*, again, as with the morphological characters, there is the problem of finding a tetraploid other than *D. elatum* in the gardens of Europe—a tetraploid, moreover, both of whose genomes of the haploid complement are similarly differentiated.

Analysis of pairing homologies of the chromosomes has proved illuminating in some respects, though not so useful in others. This was not unexpected, since in polyploids above the tetraploid level all combinations of autopolyploidy, segmental allopolyploidy, and amphiploidy may exist within a single individual (Stebbins, 1947, 1950).

The triploid hybrids were found to exhibit neither the complete absence of pairing characteristic of the progeny of crosses between very distantly related species, nor the relatively complete pairing of some segmental allopolyploids, or of autopolyploids. True, as has been pointed out, the low metaphase chiasma frequency of the chromosomes would ordinarily prevent trivalent formation by all except the large *A* and *B* chromosomes, but the actual number of univalents was ordinarily higher than the eight expected if heterogenetic pairing either between *grandiflorum* and *elatum* chromosomes or within the *elatum* complement were of regular occurrence. Actually, the formation of occasional trivalents by the large chromosomes indicates that such pairing as does occur is a mixture of the two sorts.

It has repeatedly been noted that pairing of chromosomes in the F_1 of such a species cross cannot be taken to indicate that a polyploid derivative of the cross (here a hexaploid) would necessarily be characterized by corresponding multivalent formation (Darlington, 1937; Goodspeed and Bradley, 1942; Clausen, Keck and Hiesey, 1945; Stebbins, 1947, 1950). Rather, after doubling has occurred, differential affinity of the chromosomes may result in regular bivalent formation, not only in allopolyploids (Clausen and Goodspeed, 1925; Buxton and Newton, 1928; Kagawa and Nakajima, 1933) but even in known autopolyploids (Skirm, 1942).

Since each case must be considered individually and the direct hexaploid derivative has in this instance not been produced, the triploids can best be described as being the sort of plants which might well give rise to segmental allopolyploids, the low chiasma frequency of whose chromosomes would, on the whole, lead to more-or-less regular bivalent formation in the hybrid. One should expect, then, relatively little segregation in future generations, and the plants would continue to possess the more-or-less intermediate appearance of the triploids.

The cytology of *Delphinium Belladonna* itself suggests that this species behaves rather like a segmental allopolyploid, but with perhaps fewer aberrations than are generally found in polyploids of this type. Thus, while at first metaphase, pairing is primarily by bivalents, still the formation of univalents is not uncommon. Multivalents are rarely found.

A consequence of univalent formation in gametogenesis is the production of numerous aneuploids. The mere occurrence at the polyploid level of viable aneuploids of good fertility is not unknown (Sears, 1944; Clausen and Cameron, 1944), although their high frequency here was not anticipated. In *Triticum aestivum* and *Nicotiana tabacum*, most of the nomosomics and nullisomics are individually recognizable, and this has been found to be true in certain other polyploid hybrids where aneuploids have been found (*Primula kewensis*, Newton and

Pellew, 1929; *Nicotiana tabacum*, Clausen and Goodspeed, 1924; *Nicotiana rustica*, Lammerts, 1932; *Nicotiana glauca* × *N. Langsdorffii*, Kostoff, 1939). However, while a part of the variability within *Belladonna* may be owing to aneuploidy, still it has not been possible to isolate any characteristic monosomic phenotypes, even for the large chromosomes, suggesting that there must be a considerable amount of duplicated chromosomal and genetic material in *D. Belladonna*.

This conclusion is corroborated by a survey of the extent of hypoploidy which *Belladonna* tolerates. Plants having from 43 to 44 chromosomes, while apparently infertile, are not themselves weaker than their euploid sibs. In most allopolyploids with fully differentiated genomes, such aneuploids as occur are usually deficient for no more than one or two chromosomes (Newton and Pellew, 1929; Müntzing, 1937). It is in plants in which the genomes contain many homologous chromosomes or chromosomal segments that extreme aneuploids have generally been found (Müntzing, 1937; Myers and Hill, 1940; Myers, 1947; Love and Sunneson, 1945).

Since the univalent chromosomes are usually included in the daughter nuclei, the prevalence of hypoploids among the plants of all the *Belladonna* populations studied can be explained on the assumption that in these relatively balanced plants, a gamete deficient for one or several chromosomes is at an advantage over gametes containing chromosomes in excess. Therefore, those gametes which function would then include 24 or fewer chromosomes. It is not, however, to be concluded that *Belladonna* is insensitive to chromosome losses of indefinite extent: on the whole, aneuploids with 46 or 47 chromosomes are the most frequent, so that functional gametes must not, as a rule, lack more than one or two chromosomes. Further, though intervarietal crosses are easily made, the germinability of seeds produced is higher in selfs than in intervarietal crosses (Table XI). It seems, therefore, that such chromosomal differentiation as exists between varieties may result in sufficient deficiencies either in the embryo or in the endosperm that in consequence the hybrid seed is less viable. Finally, since fertility tends to be generally higher in the more nearly euploid individuals, and the progeny of the aneuploids do not vary more in chromosome number than do the progeny of normal individuals, *D. Belladonna* Hort. maintains itself approximately at the hexaploid level.

Of the many allopolyploids which have been analyzed (Stebbins, 1947, 1950) the one perhaps most similar to *D. Belladonna* is the segmental allopolyploid *Anemone Jancewskii* (= *A. sylvestris* × *A. multifida* var. *magellanica*), first synthesized by Jancewski before 1892, resynthesized by Gajewski (1946), and further, occasionally spontaneous in botanic gardens. Morphologically, the hybrid is intermediate between the parents and is quite constant, even aneuploids not being of abnormal appearance. A cytological study of the parents and the hybrids by Gajewski revealed that in the triploid (24 chromosomes) at MI from 3 to 8 bivalents are formed, the remaining chromosomes being unpaired. In the F_2 generation produced by the functioning of unreduced gametes (Jancewski reported two instances of somatic doubling but Gajewski did not obtain any hexa-

ploids by this means), in addition to cells in which 24 bivalents occur, in other cells there were some univalents and from 1 to 3 multivalents. Seed and pollen fertility in different individuals of this generation ranged from rather high to rather low, and in the F_3 there was a general increase in fertility. The chromosome numbers were uniformly about 48 in Gajewski's plants, but in the accessions from botanic gardens they ranged from 42 to 48. The chief respect in which *A. Jancewskii* seems to differ from *D. Belladonna* and from the hybrids synthesized here is in the complete absence of trivalents in the triploid and in the higher frequency of multivalents in the hexaploid. The first may be due to greater differentiation of the parental genomes; the second may well be the result of the much higher chiasma frequency of the chromosomes of this hybrid.

To summarize, then, although *D. Belladonna* has previously been considered an amphidiploid on the basis of its largely regular meiosis and its relatively constant appearance, intermediate between certain diploid and tetraploid species of cultivation, the garden hexaploid has been shown to have somewhat less regular meiosis than is characteristic of true amphidiploids. This is indicated both by the common occurrence of univalents and other irregularities in meiosis, and in the higher production of viable, fertile aneuploids than is characteristic of such plants. Rather, *D. Belladonna* may better be classed as a segmental allopolyploid, in which the low chiasma frequencies of the chromosomes tend to enforce bivalent formation, and morphological constancy is further enhanced by the quantitative mode of inheritance of many of the differentiating characters.

DERIVED HEXAPLOIDS

For descriptive purposes, all of those plants having in their ancestry one of the triploids and *Belladonna* have been termed "derived hexaploids." The pedigrees of the major lines are given in text-fig. 2.

First-generation Hybrids: Triploids × *Belladonna Varieties.*—

The dangers of making decisions regarding the nature of polyploidy in a hybrid, whether it be a segmental allopolyploid or an amphiploid, have been pointed out by Stebbins (1947, 1950). Neither external morphology of the chromosomes nor the nature of chromosome association can be used as a single criterion in identifying the chromosomes of a hybrid. Therefore, whenever it is at all possible, "the form in question should be hybridized with its putative diploid ancestor or ancestors, or better yet, it should be resynthesized." However, since repeated attempts to produce hybrids between *Belladonna* and either *D. grandiflorum* or *D. elatum* have been unsuccessful and direct doubling of the chromosome number of the triploids has not been achieved, a compromise has been made in the production and study of hybrids between the triploids and Smith's *Belladonna.*

By using the triploids as female parents and pollinating them with *Belladonna* 23 F_1 seeds were obtained, of which 7 yielded plants which reached maturity. Unfortunately, these hexaploids, which are of the greatest interest in this study, are not known in as great detail as is desirable, since all but one were lost in the

TABLE VIII

MEIOSIS IN THE DERIVED HEXAPLOIDS

Plant	Chromosome Number	Metaphase I					Anaphase I					Anaphase II				
		Number of cells	Number bivalents per cell–range	Total number multivalents	Number multivalents involving intermediate chromosomes	Median number bivalents	Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells		Number of cells	Cells with laggards	Cells with other abnormalities	% abnormal cells	
51-213-3	48, 2F	43	24–19	3	1	23	139	6	13	13.7		60	9	2	18.3	
51-216-6	49, 2F	6	24–20	2	0	—	—	—	—	—		—	—	—	—	
51-216-10	50 (7A)	29	24–22	8	2	24	45	Largely regular		11.1		About 15% irreg.			—	
51-216-16	50 (7A)	31	24–20	4	0	24	65	9	9	27.7		37	2	—	11.2	
51-219-4	46	55	22–17	0	0	21	50	8	2	20.0		—	—	—	—	
51-220-4	48	10	23–20	1	0	—	25	3	2	20.0		—	—	—	—	
51-221-11	48	20	24–21	0	0	23	82	8	8	19.5		70	5	13	25.7	
51-222-21	47	33	23–20	1	0	21	83	17	4	25.0		45	7	5	26.6	
51-222-38	48	23	24–21	0	0	23	32	7	5	37.3		22	7	3	45.4	
51-223-5	47	33	23–21..	2	1	23	—	—	—	—		—	—	—	—	
51-223-31	44	7	22–17	0	0	—	61	8	2	16.7		36	7	5	25.0	

unusually severe winter of 1951-52 following their first flowering, and most of the meiotic material available for study was a few buds embedded in paraffin.

Of the plants which were surveyed, 50-20-1 (48-6-2 × Smith's *Belladonna*) formed mostly bivalents at MI, but 6–12 univalents were commonly present, and reduced chiasma frequency in the long chromosomes was observed. At first anaphase, abnormalities were observed in 28.0 per cent of the cells studied, but in only 10.0 per cent of cells at anaphase II. Pollen viability was 41.4 per cent, and a fair amount of seed was set both by selfing and by backcrossing to *Belladonna*.

51-209-1 (48-27-5 × Smith's *Belladonna*) exhibited fairly regular pairing at MI. Usually no more than 4 univalents were found, and frequently 24 bivalents were present. Anaphase I was visibly normal in about 45 per cent of all cases, and AII was somewhat more regular. Pollen viability was in the neighborhood of 85 per cent. This plant produced a heavy set of viable seed, whether selfed or further backcrossed to *Belladonna*.

51-213-1 (50-15-4 × Smith's *Belladonna*) was studied in sectioned material, in which only approximate counts could be obtained. There was apparently relatively good pairing at MI—many PMC's appeared to be quite regular, and usually no more than 4 univalents were evident. Several times, a single trivalent involving one of the larger chromosomes was observed. AI's were regular in 60 per cent of the cases, as were most of the AII's. Pollen viability was as high as 91 per cent. Again, both selfs and backcrosses to *Belladonna* proved successful. A sister seedling, 51-213-2, showed metaphase pairing with generally 2–4 univalents, the remaining chromosomes being in bivalent configurations. AI segregation in this plant appeared to be about 55 per cent normal.

51-213-3, studied in some detail (Table VIII), had at least 23 bivalents in two-thirds of the cells at MI, and both anaphase divisions were highly regular. Little trivalent formation was recorded, however.

Two other hexaploids, 51-211-1 and 51-211-2 (50-15-1 × Cliveden Beauty), could not be analyzed; of these, the former yielded a good set of seed upon selfing. The other plant was not pollinated.

The advanced generations among the derived hexaploids had their origin, as may be seen in text-fig. 2, from five F_1 individuals. Of these, two of the parental triploids had different white *elatum* parents but the same blue *grandiflorum* parent, while the triploid parent of the third line was the offspring of an azure *elatum* variety and the fragment-bearing cobalt diploid, 47031-1. In general, as will be seen, the lines derived from the last cross are distinct in cytological behavior from the other two.

Somatic Chromosome Morphology.—

Because of the number of plants represented by these populations, studies of somatic chromosomes have been restricted to root-tip counts. The total number of each of the easily identified *A* and *B* chromosomes was counted, gross morphological alterations of the chromosomes were noted, and in instances where staining was good enough, average satellite number and disposition were determined.

TABLE IX

CHROMOSOME NUMBER IN *D. BELLADONNA* AND THE DERIVED HEXAPLOIDS

	Line	Hypoploids								Hyperploids								48 chromosomes	
		Aneuploid only	Fragment only	5A	5B	7A	7B	Other	Total	Aneuploid only	Fragment only	5A	5B	7A	7B	Other	Total	Fragment	Normal
51–216		0	2	0	0	0	0	7A, 7B—1	3	2	5	0	0	6	0	8A—2 7A, 7B—1 7A, 7B—1	16	4	1
51–217		1	0	0	0	1	0	0	2	0	0	0	0	3	1	0	4	1	2
51–218		0	4	0	1	0	0	0	5	0	9	0	0	0	0	0	10	8	3
51–219		7	0	0	1	0	0	0	8	0	0	0	0	0	0	0	0	0	4
51–220		6	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	1
51–221		5	0	1	0	0	0	0	6	4	0	0	0	0	1	0	5	1	13
51–222		8	0	0	1	0	1	0	10	5	0	0	0	2	0	0	8	0	27
51–223		8	0	0	0	0	0	0	8	3	0	0	0	0	0	8A—1	3	0	9
51–224		6	0	0	1	0	0	0	7	0	0	0	0	0	0	0	0	0	8
52–311		15	1	0	0	0	0	0	18	1	0	0	0	0	1	0	1	0	6
51–232		10	1	1	0	0	0	0	12	2	0	0	0	0	0	0	2	0	11

As to the number of satellites present, the chief difference noted among the various populations was in the expression of the *A*-SAT, which is potentially present on two of the 6 *A* chromosomes in all lines, since the triploid and the *Belladonna* parent each should have contributed one. However, while plants in the three populations descended from the 51-213 individuals usually revealed one or two satellited *A*'s, this satellite was not strongly manifested by the other populations. Apparently, this difference had its origin in the triploid parents, since, as was mentioned above, the 50-15 individuals were characterized by possessing a more "active" *A* than the other lines.

Aneuploidy is common in all populations, as it is within *Belladonna;* however, the various lines have characteristic differences (text-fig. 7, Tables IX and X). Thus, while *Belladonna* populations contain many hypoploids with as few as 41 chromosomes and only occasional hyperploids, this pattern occurred only in 51-219 and 51-220 (51-202-3 × self, and × Smith) among the derived hexaploids. A somewhat intermediate situation was found in 51-222 and 51-223 (51-209-1 × self, and × Smith) and in 51-221 (51-202-7 × 50-20-1) in which plants with 48 chromosomes were frequent and both hypoploids and hyperploids occurred. A third situation was found in lines 51-216, 51-217, and 51-218, derived from the fragment-bearing individuals 51-213-1 and 51-213-2. In these populations, hyperploid individuals were most numerous, though an occasional plant with as few as 45 or 46 chromosomes was found. In addition, the centric fragment was quite common, being found in 17 out of 24 individuals of 51-216, and 23 of 26 individuals of 51-218. In 51-217, which was a backcross to Smith's *Belladonna*, the fragment occurred in 4 of 8 individuals examined. The exact number of fragments present in each individual is not given, since the fragment does not always segregate regularly and may occasionally vary from root-tip to root-tip

TABLE X
IRREGULAR DISTRIBUTION OF CHROMOSOMES IN THE HEXAPLOIDS

Line	Number of plants	Number chromosomes deficient			Number chromosomes in excess		
		A	B	Other	A	B	Other
51–216	24	0	0	8	11	1	17
51-217	9	0	0	2	4	1	3
51–218	26	0	1	7	0	1	14
51–219	12	0	1	18	0	0	0
51–220	7	0	0	12	0	0	0
51–221	24	0	1	7	0	1	6
51–222	45	0	1	18	4	0	6
51–223	20	0	0	14	0	0	3
51–224	15	0	1	16	0	0	0
52–311	25	0	1	49	0	1	0
51–232	25	1	0	22	0	0	2
Total	232	1	6	173	19	5	51

of a given plant. It is not known to what extent it may be possible to accumulate fragments in future generations, but in samples of two F_3 populations, each of whose progenitors bore two fragments, no more than three fragments were observed in a total of fifteen individuals; on the other hand, all but one of the remainder possessed one or two fragments. Since transmission of the fragment through both the pollen and the ovule has been demonstrated (in the pollen, on the diploid and hexaploid levels, and in the ovule, on the triploid and hexaploid levels), it may well be that the failure to find many individuals with an augmented fragment number reflects some lethal effect of numerous fragments. It may be noted that the formation of isochromosomes by misdivision of the fragment, such as was noted by Darlington in *Fritillaria* (1940) and by Rhoades in *Zea* (1940) has never been observed here, although such a chromosome should be easily recognized by its distinct morphology.

Fertility of the Derived Hexaploids.—

A systematic study of all the plants has not been made, since they number now well over 1000. As has been noted above, the initial triploid × hexaploid hybrids were of good fertility. In succeeding generations (to the F_4 and various backcrosses to *Belladonna*) plants exhibiting all degrees of fertility have been found, as evidenced particularly by seed set.

Detailed meiotic studies have been made in only a few of these plants (Table VIII), but the degree of pairing has generally been found to agree well with that characteristic of *D. Belladonna*. Thus, 51-221-11 forms no more than 6 univalents and usually only 2 at MI; no multivalents were noted; and both anaphases are fairly regular. A similar situation, with slightly more numerous irregularities in the anaphases, was found in 51-222-38. In aneuploid individuals, irregularities were, to be sure, more frequent. Thus, 51-216-10 and 51-216-16, both of which possessed an *A* chromosome in excess as well as one other excess chromosome, often formed 24 bivalents, but were also characterized by low multivalent formation, chiefly involving the extra *A* chromosome. A hypoploid (51-219-4; 46 chromosomes) averaged 21 bivalents, but the anaphases were not especially irregular. As in *Belladonna*, the number of laggards at anaphase was always much less than that of univalents at metaphase.

While infertile plants have been found both among the aneuploids and among apparently normal plants with 48 chromosomes, a study of seed germinability among those plants which have set some seed shows that, on the whole, the highest number of viable seeds were produced by plants with 48 chromosomes. However, even in this group, germinability ranged from 0 to about 90 per cent, and, with one exception, the production of seed with at least 40 per cent germinability was confined to plants having 47–49 chromosomes (Table XI).

Segregation in the Derived Hexaploids.—

On the whole, each line within this group exhibits considerable uniformity by the F_3 (or equivalent) generation. However, there are few individuals in each

TABLE XI

SEED GERMINABILITY IN *DELPHINIUM BELLADONNA* AND DERIVED HEXAPLOIDS

Plant	Chromosome number	Number seeds sown	Number seedlings	% Germinability
Smith × self	48	27	21	78
Smith × Bellamosum	48 × ?	86	25	29
Lamartine × self	48	24	14	57
Lamartine × Smith	48 × 48	52	8	17
51-216-3 × self	48	4	0	0
51-216-4 × self	49, 2F	2	0	0
51-216-12 × self	48, 2F	75	15	20
51-216-13 × self	52	15	0	0
51-218-2 × self	49, F	8	3	37
51-218-9 × self	48	14	2	14
51-218-16 × self	48, 3F	42	23	55
51-218-18 × self	49, 2F	2	0	0
51-218-19 × self	46, 2F	29	18	62
51-218-29 × self	50, 2F	68	23	34
51-218-39 × self	48, F	8	2	25
51-221-2 × self	49	50	30	60
51-222-11 × self	48	3	0	0
51-222-13 × self	47	36	4	11
51-222-19 × self	48	11	0	0
51-222-28 × self	48	4	0	0
51-222-7 × self	48	200	165	82
51-222-8 × self	48	47	21	44
51-222-14 × self	48	23	17	73
51-222-36 × self	48	12	0	0
51-222-37 × self	48	32	14	44
51-222-43 × self	47	22	3	13
51-222-46 × self	48	8	1	13
51-222-50 × self	46	33	16	48
51-222-54 × self	49	20	1	5
51-222-61 × self	48	22	13	59
51-222-67 × self	48	5	0	0
51-222-77 × self	48	9	4	45
51-222-95 × self	49	15	7	47
51-222-100 × self	48	7	1	14
51-223-1 × self	49	3	0	0
51-223-21 × self	48	10	6	60
51-223-22 × self	48	15	5	33
51-223-38 × self	48	14	5	34
51-223-44 × self	47	7	0	0

group which deviate noticeably from the rest, especially in leaf shape. In only one instance (an F_3 family derived from 51-209) have more than a few individuals deviated in the direction of either *D. grandiflorum* or *D. elatum*, and the variation here is in the direction of rather more finely dissected leaves than generally occur in *D. Belladonna*. Taken as a whole, however, the general aspect of the assemblage is that of a *Belladonna* population in which a few individuals are more or less branched, shorter or taller, or with leaves more or less finely dissected than in *D. Belladonna* Hort. (pl. 10).

Color inheritance in these forms is such as to raise some interesting questions, but detailed treatment of this subject will be reserved for future consideration.

Discussion and Summary.—

Although the analysis of meiosis in the first-generation hybrids was not complete, it is still clear from the above that while somewhat more irregular than in *Belladonna*, the meiotic process does not appear to be greatly disturbed, and in only one individual (51-213-1) was the regular production of multivalents noted.

Chromosome numbers among the progeny of these plants suggest for the various crosses what homologies and disharmonies may have been operative in their parents. Crosses 51-219-, 51-220-, and 51-223- are most similar to *Belladonna* in that chiefly euploids and hypoploids were produced. In the first two of these lines, which represent the self and backcross to Smith's *Belladonna*, respectively, of the F_2 of the cross 48-6-2 × Smith's *Belladonna*, there has been no intentional building up of the *Belladonna* complement by backcrossing. Therefore, unless the introduced chromosomes of the triploid have been appreciably eliminated, no strong barriers of chromosomal differentiation appear to exist between the parental triploid and *Belladonna*. The aneuploidy thus seems to be of the same nature as in *D. Belladonna* Hort.

On the other hand, 51-223 is a first backcross to Smith's *Belladonna* of the original hybrid between 48-27-5 and Smith's *Belladonna*. Since the same hybrid when selfed gave rise to line 51-222 (in which both hyperploids and hypoploids were frequent, and in which excessive numbers of supernumerary *A* chromosomes were found), it seems in this case that occasional formation of multivalents involving the large chromosomes must occur, and perhaps that more pronounced structural differences may exist between the parental genomes than in the previous instance. The first conclusion is based on the occurrence of 4 *A* chromosomes out of a total of 10 chromosomes extra in the hyperploid individuals of line 51-222, more than three times the expectancy if this chromosome were segregated irregularly only as often as the small chromosomes, and even more unlikely as a random event if the higher chiasma frequency of this chromosome is considered.

In the absence of any indication of multivalent formation by the smaller chromosomes, it is necessary to assume that some other factor is operative in producing individuals possessing these chromosomes in excess. This may be accounted for if gametes hyperploid for these chromosomes are not at the selective disadvantage which appears to occur in *D. Belladonna*. Such an hypothesis can best be explained if certain euploid combinations in these individuals are actually deficient for necessary genetic material, which may be supplied by the extra chromosomes.

The extreme frequency of hyperploidy in the 51-213 derivatives, where hyperploids represent the bulk of the populations, seems to indicate both high multivalent formation by the *A* chromosomes, occasional multivalent formation by the *B* chromosomes, and to a greater extent than in the preceding case, the operation of some factors which favor the functioning of gametes hyperploid for the smaller

chromosomes. This is particularly true of 51-216 and 51-217, the F_2 and first backcross respectively of 51-213-1, the plant in which multivalents were noted above. That transmission of the excess large chromosomes may be through the pollen grain as well as through the egg is suggested by the fact that a comparable excess of large chromosomes was present in 51-217, the backcross line, as compared with 51-216.

As to the fertility of the derived hexaploids, it has already been noted that euploid chromosome numbers and fertility are not necessarily related, but that, on the whole, more plants which yield seeds with good germination have about 48 chromosomes than have chromosomes either much in excess or in deficiency of this number. The tendency to preserve the hexaploid number appears to be almost as strong as in the *Belladonna* lines themselves.

So far as the homologies of the genomes derived from triploid and hexaploid sources are concerned, it seems that they must be very nearly similar, since there has been no strong morphological or cytological disharmony in the derived hexaploids as compared with *D. Belladonna*. In fact, the differences are very slight indeed if one contrasts the behavior of these plants with that of the intervarietal crosses between *Belladonna* and Bellamosum. Although the latter variety was derived from the former, yet reduced seed germinability and more frequent aneuploid production have been found to occur in their hybrids than characterize either variety when it is selfed.

General Discussion

It is concluded that *D. Belladonna* Hort. is an allopolyploid hybrid between the tetraploid species *D. elatum* L. and the diploid species complex of *D. grandiflorum* L. In general, *D. Belladonna* may best be classed as a complex segmental allopolyploid, but it should be emphasized that classification is especially difficult since strong chromosomal barriers to hybridization do not seem to exist between even distantly related species of *Delphinium* (e.g., *D. elatum* and *D. nudicaule* or *D. cardinale*). Unlike many other segmental allopolyploids, however, *D. Belladonna* is easily distinguished from both parents. It has already been suggested that regularity in pairing, enforced by differential affinity of the chromosomes, as well as by the not insignificant effect of low chiasma frequency, is probably responsible in large part for this behavior. Moreover, the quantitative mode of inheritance of many of the characters tends to keep *D. Belladonna* in its intermediate morphological position between the parents.

Undoubtedly, a large part of the success of *D. Belladonna* (as opposed to the frequent failure of such hybrids to be perpetuated in nature; Clausen, Keck and Hiesey, 1945) has been the result of its being a garden plant. Thus, in the first place, it was vegetatively propagated for an unknown number of years before the first occurrence of fertility was reported; second, it has been subject to the care and selection of gardeners and plant breeders over the years, so that the difficulties (for instance, multivalent formation by the large chromosomes) such a hybrid would encounter during the first few generations in nature were mostly obviated.

Several explanations may be offered to account for the *elatum* tendencies noted in the experimentally produced triploids. First, while *D. grandiflorum* has a number of varieties, those varieties grown in gardens are, on the whole, similar with respect to the features which they contribute to the phenotype of *Belladonna*—the large self-colored bee, the wide open flower, the few-flowered inflorescence, the finely dissected leaves, and much-branched habit. *D. elatum*, on the other hand, exists in many natural and horticultural variants; probably a *D. elatum* bred for a showy "bee," with a relatively open inflorescence and rather narrow leaf segments, would yield offspring of the type characteristic of *Belladonna* when such a variety was crossed with *grandiflorum*. However, the *elatum* variety Summer Skies, seed parent of triploids 50-15, has a small bee, broad leaf segments, and very dense strong main spike with numerous flowers; the triploids plotted in text-fig. 5 are indeed intermediate with respect to their known parents. All one can say of the presumptive *elatum* parent of *Belladonna* is that it was almost certainly a smaller, less extreme variety than those grown today, judging from historical plates of Delphiniums cultivated in the middle of the last century.

The question of the nomenclature of the triploid and hexaploid garden Delphiniums may be viewed in three very different aspects: first, as it concerns the taxonomist, second, the geneticist, and third, the gardener or nurseryman. While the first two views may be reconciled to a certain extent, the unfortunate truth is that the people most concerned with these Delphiniums (which are, after all, cultivated plants) will probably perpetuate the past errors and contribute new cases of mistaken identity in the future.

For the geneticist, it is desirable that the exact parentage, insofar as it is possible, be given for every hybrid where it is known. Convenience in the herbarium, on the other hand, requires that some category be devised which will adequately contain the assemblage. Thus, according to the International Code of Botanical Nomenclature (Lanjouw, ed., 1952), "hybrids or putative hybrids between two species of the same genus are designated by a formula, and whenever it seems useful or necessary, by a name." In the latter case, the specific name is to be preceded by "×." Further, where different hybrids of the same parentage exist, they may be united in a collective taxon in which the forms are recognized as nothomorphs, "designated by an epithet preceded by the binary name of the hybrid group and the term "nothomorph." While the general practice in systematics is to give priority to the earliest validly published name, for cultivated plants provision is made that the most generally employed name may be used. Of the early names applied to hybrids of *D. grandiflorum* and *D. elatum*, only *D. formosum* and *D. Belladonna* are in wide usage. Since the name *Delphinium formosum* was given in 1856 to a wild species (Boissier and Huet), it seems advisable to maintain *D.* × *Belladonna* Hort. *ex* Bergm. (see footnote, p. 119) as the epithet of the hexaploid Delphiniums and their triploid allies. Varieties such as Lamartine, Capri, *Moerheimi*, and the triploids and derived hexaploids of this study may then be considered as nothomorphs of this species.

SUMMARY

1. Previous workers have postulated that *D. Belladonna* Hort. originated either as a variety of *D. cheilanthum* Fisch. *ex* DC., or as a hybrid of *D. cheilanthum* with some unknown other species, or by hybridization between such diploid and tetraploid species as *D. grandiflorum* L. and *D. elatum* L. It is pointed out that solution of the problem must be based upon a combination of methods, including historical research, morphological analysis, and cytogenetic data.

2. A study of the taxonomic and horticultural literature indicates that *D. cheilanthum* is a coherent diploid species, rare in gardens, native to Siberia, Mongolia, and Kumaon (China), with relatives in adjacent areas; *D. Belladonna*, on the other hand, is a hexaploid, known only in gardens, where it has arisen upon different occasions.

3. Hybrids between various lines of *D. elatum* and *D. grandiflorum* var. *chinensis* have been produced and have been found to be morphologically comparable to *D.* × *Belladonna* Hort. *ex* Bergm. and, moreover, within the limits imposed by their triploid condition, interfertile with the "species."

4. Character analysis of the various species and hybrids indicates that both *Belladonna* and the experimentally produced triploids are intermediate with regards to *D. elatum* and *D. grandiflorum*, but that *D. cheilanthum* is morphologically and cytologically distinct from *D. Belladonna* and could not have been the diploid parent of the latter if *D. elatum* was the tetraploid parent.

5. Methods are given for the study of somatic and meiotic chromosomes and of pollen mounts.

6. It is pointed out that for the species and hybrids studied, size of pollen grain may be used as an indicator of polyploid level in both living plants and herbarium material.

7. Study of the morphology of the somatic chromosomes has shown that the genomes of the two diploid types which have been considered possible parents of *D. Belladonna* may de distinguished on the basis of their satellite distribution. In *D. grandiflorum*, satellites occur on chromosomes *C* and *H*, while in *D. cheilanthum* the *A* and the *C* chromosomes are satellited. Further, the length of the satellited arm of chromosome *A* in *D. cheilanthum* is longer than the corresponding arm of the same chromosome in *D. grandiflorum*, suggesting that there has been a translocation of the satellite-bearing segment in the evolution of the genome.

8. Differential activity of the satellites was found to characterize even the diploid species: in *D. grandiflorum* the *C* satellite is about twice as "active" as the *H* satellite; in the closely related *D. tatsienense*, both are equally active. In *D. cheilanthum* the *A* satellite is about twice as active as the *C* satellite.

9. The tetraploid species *D. elatum* was found to have a gametic complement corresponding to the summation of the *grandiflorum* and the *cheilanthum* genomes. Amphiplasty of the *H* satellite occurs.

10. In all of the experimentally produced triploids the potential satellite number was found to be 1 *A*, 3 *C*'s, and 2 *H*'s, but in triploids of lines 48-27 and

48-6, the *A* satellite was rarely evident on account of amphiplasty. The morphology of the chromosomes of *Belladonna* supports the hypothesis of similar parentage for these types, since the total *Belladonna* complement has double the potential satellite number of the triploids. In both the triploids and in *Belladonna*, amphiplasty of the *A* satellite was found in some individuals.

11. Meiosis in *D. grandiflorum* and *D. elatum* is largely regular, the chromosomes forming bivalents (rarely some univalents in the latter species) and assorting on the whole regularly.

12. In the triploid hybrids, prophase and metaphase pairing is chiefly in univalents and bivalents, trivalents being formed only rarely and only by the *A* or *B* chromosomes. Chiasma frequency is somewhat reduced and both intergenomal and intra-genomal pairing of the chromosomes occurs. Bridges and fragments are characteristic of both anaphase divisions, although the number of chromosomes lagging at anaphase is considerably less than that of univalents at metaphase. Micronuclei are frequent, and rare viable unreduced pollen grains are produced.

13. Meiosis in *Belladonna* is more or less regular, but the production of univalents commonly occurs, and aneuploid gametes are produced and function. Chromosome numbers as low as 41 have been found, but ordinarily only those plants with about the hexaploid number are fully fertile. It is suggested that *D. Belladonna* is a segmental allopolyploid which preserves a uniform appearance because low chiasma frequencies of the chromosomes enforce bivalent formation and because of the quantitative mode of inheritance of many characters.

14. Lines of derived hexaploids have been produced by pollinating various triploids with pollen of Smith's *Belladonna*, and further selfing or backcrossing of the plants produced. On the whole, these lines are only slightly more variable than is *D. Belladonna*, and fertility is only slightly impaired as compared with that "species." A small amount of multivalent formation characterizes some of these lines.

15. It is concluded that *D.* × *Belladonna* Hort. *ex* Bergm. embraces the entire assemblage of present-day varieties derived from crossing *D. elatum* with *D. grandiflorum*, as well as a number of hybrids of the last century which are no longer in cultivation.

16. A telocentric fragment has been transmitted from a *D. grandiflorum* pollen parent through four generations. No isochromosomes have been observed.

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APPENDIX

CHROMOSOME NUMBERS OCCURRING IN THE SPECIES OF *DELPHINIUM*

Species	2n number	Author and date
Ajacis L.	16	Langlet, 1927; Tjebbes, 1927; Gregory, 1941
Andersoni Gray	16	Lewis *et al*, 1951
azureum Michx.*	32?	Lewitsky, 1931; Gregory, 1941
Belladonna Hort.	48	Langlet, 1927; Lawrence, 1936; Propach, 1939, 1940
Blochmanae Greene	16	Lewis *et al*, 1951
brachycentrum Ledeb.	16	Langlet, 1932
Brunonianum Royle	16	Lewitsky, 1931; Propach, 1940
bulleyanum Forrest	32	Gregory, 1941
californicum T. & G.	16	Lewis *et al*, 1951
cardinale Hook.	16	Propach, 1940; Mehlquist, 1943; Lewis *et al*, 1951
cardiopetalum D.C.	16	Tjebbes, 1927; Lewitsky, 1931; Gregory, 1941
carolinianum Walt.*	32?	Gregory, 1941
cashimirianum Royle	16	Propach, 1940
caucasicum C. A. Mey.	16	Gregory, 1941
cheilanthum Fisch. *ex* DC.	16	Propach, 1939
Consolida L.	16	Hocquette, 1922; Tjebbes, 1927; Langlet, 1927; Lewitsky, 1931; Gregory, 1941
cuyamacae Abrams	16	Lewis *et al*, 1951
decorum Fisch. and Mey, ssp. *Tracyi* Ewan	16	Lewis *et al*, 1951
Delaveyi Franch.	16	Lewitsky, 1931; Propach, 1940
Duhmbergi Huth	32	Lewitsky, 1931
	16	Propach, 1940
elatum L.	32	Lewitsky, 1931; Propach, 1940; Gregory, 1941
fissum Waldst. & Kit.	32	Hocquette, 1922; Propach, 1940
flexuosum Raf.	32	Gregory, 1941
formosum Boiss. & Huet.	32	Gregory, 1941
gayanum Willmott	16	Gregory, 1941
glaucum Wats.	16	Lewis *et al*, 1951
gracilentum Greene	16	Lewis *et al*, 1951
grandiflorum L.	16	Propach, 1940

* Mehlquist (unpublished) has determined these American species as diploid. His studies were of plants from the native habitat, whereas the other determinations were probably made from material sent out from European botanical gardens, which often confuse *D. elatum* with *D. carolinianum* and *D. azureum*.

Species	2n number	Author and date
gypsophilum Ewan	16, 32	Lewis *et al*, 1951
Hansenii Greene	16, 32	Lewis *et al*, 1951
hesperium Gray	16	Lewis *et al*, 1951
hesperium f. *pallescens* Ewan	16	Lewis *et al*, 1951
ilienae Huth	16	Propach, 1940
inopinum (= *D. parishii* var. *inopinum* Jeps.)	16	Lewis *et al*, 1951
Lamartine Hort.	48	Lawrence, 1936
Moerheimii Hort.	24	Lawrence, 1936
nudicaule Torr. & Gray	16	Tjebbes, 1927; Propach, 1940; Gregory, 1941; Lewis *et al*, 1951
Nuttallianum Pritz.	16	Lewis *et al*, 1951
orientale (?) (*D. orientale* Losc.; *D. orientale* S. Gay)	16	Beckman, 1928; Gregory, 1941
Parishii Gray	16	Lewis, *et al*, 1951
Parryi Gray	16	Lewis, *et al*, 1951
Parryi ssp. *seditiosum* (Jeps.) Ewan	16	Lewis, *et al*, 1951
patens Benth.	16	Lewis, *et al*, 1951
Penardi Huth	16	Gregory, 1941
peregrinum L.	16	Gregory, 1941
pictum Willd.	16	Gregory, 1941
polycladon Eastw.	16	Lewis *et al*, 1951
Purpusii Brandg.	16	Lewis *et al*, 1951
recurvatum Greene	16	Lewis *et al*, 1951
Ruysii Hort	32	Lawrence, 1936
scopulorum Gray	16	Gregory, 1941
speciosum (?) (*D. speciosum* Janka = *D. elatum* L.; *D. speciosum* Bieb.)	16	Langlet, 1927
Staphisagria L.	16	Hocquette, 1922; Langlet, 1927; Lewitsky, 1931; Gregory, 1941
sulphureum Boiss. & Hausskn	16	Gage, this paper
tatsienense Franch.	16	Lewitsky, 1931; Propach, 1940
tricorne Michx.	16	Gregory, 1941
trolliifolium Gray	16	Lewis *et al*, 1951
truncatum Lang.	16	Langlet, 1927
uliginosum Curran	16	Lewis *et al*, 1951
umbraculorum nom. nud.	16	Lewis *et al*, 1951
variegatum Torr. & Gray	16, 32	Lewis *et al*, 1951
yunnanense Franch.	16	Gregory, 1941
Zalil Aitch. & Hemsl.	16	Gage, this paper

CHROMOSOME NUMBERS OCCURRING IN THE HYBRIDS DETERMINED BY H. PROPACH, 1940

Variety	Breeder or Source	Chromosome Number
Eisberg	E. Benary, Erfurt	16
Blauglut	K. Foerster, Bornim	24
Blautanne	"	24
Alpenbote	"	32
Berghimmel	"	"
Blaurake	"	"
Blickfang	"	"

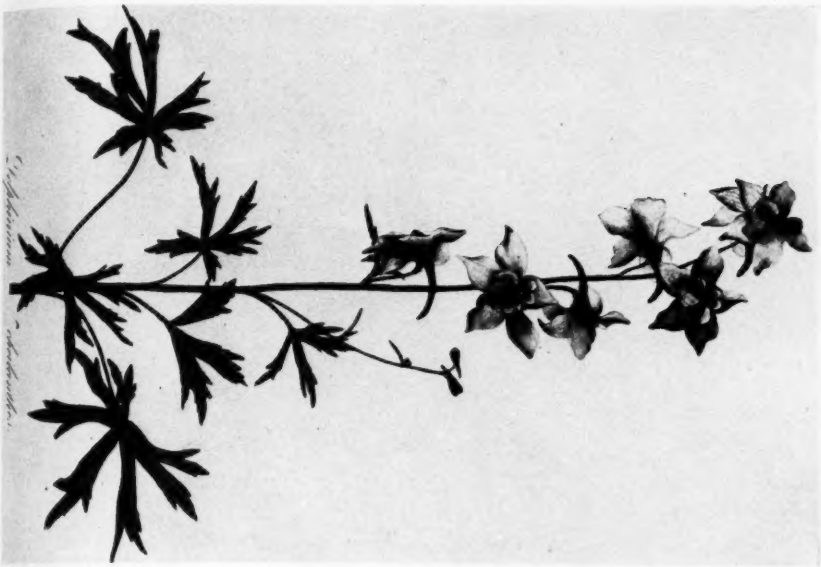
Dein blaues Wunder	K. Foerster, Bornim	32
Enzianherold	"	"
Enzianturm	"	"
Ernst von Borsig	"	"
Fön	"	"
Glasfenster	"	"
Gletscherwasser	"	"
Gnom	"	"
Grossenwahn	"	"
Gute Nacht	"	"
Havelland	"	"
Kirchenfenster	"	"
Kreuzritter	"	"
Lautsprecher	"	"
Leuchtturm	"	"
Morgenstrahl	"	"
Münsterturm	"	"
Nachtauge	"	"
Nachthorn	"	"
Nostradamus	"	"
Opalsäule	"	"
Perlmutterbaum	"	"
Purpurritter	"	"
Rosenquarz	"	"
Sontagskind	"	"
Stichflamme	"	"
Tante Clothilde	"	"
Tempelgong	"	"
Troppenacht	"	"

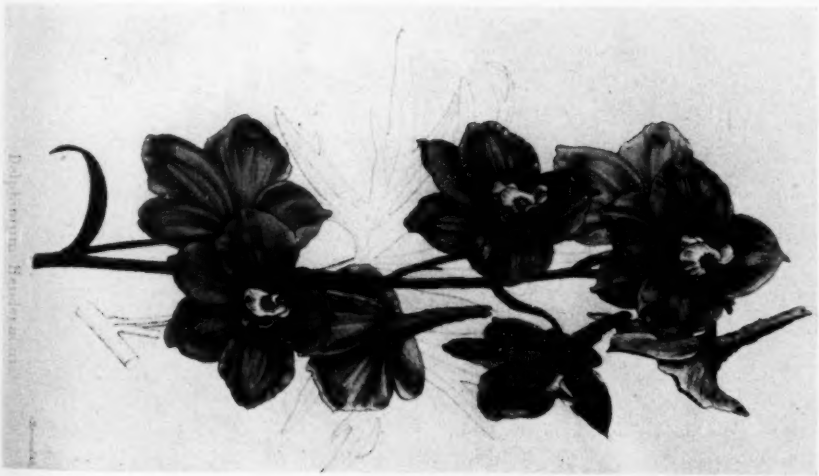
EXPLANATION OF PLATE

PLATE 7

Fig. 1. *Delphinium cheilanthum* Fisch., reproduced from von Schrank, 'Plantae Rariores Horti Academici Monacensis,' pl. 52. 1819.

Fig. 2. *Delphinium Hendersoni*, from Revue Horticole. 1854.





EXPLANATION OF PLATE

PLATE 8

Fig. 1. *Delphinium Belladonna*, Smith's selection from "Cliveden Beauty."

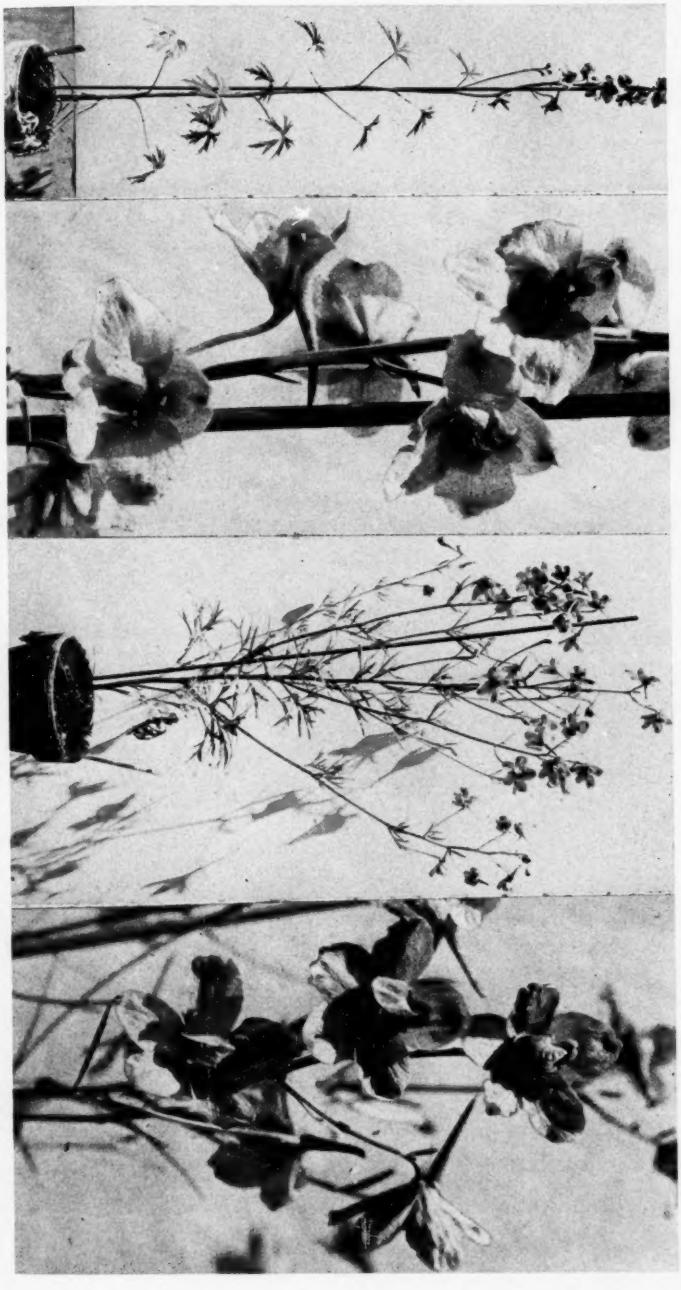
Fig. 2. *Delphinium formosum*, from Flore des Serres. 1857.

Explanation of Plate

PLATE 9

Figs. 1 and 2. Habit and detail of inflorescence of *Delphinium cheilanthum* Fisch. *ex* DC., grown at the Missouri Botanical Garden from seed received from Uppsala.

Figs. 3 and 4. Habit and detail of *Delphinium grandiflorum* L. var. *chinensis* Fisch., "Blue Butterfly."



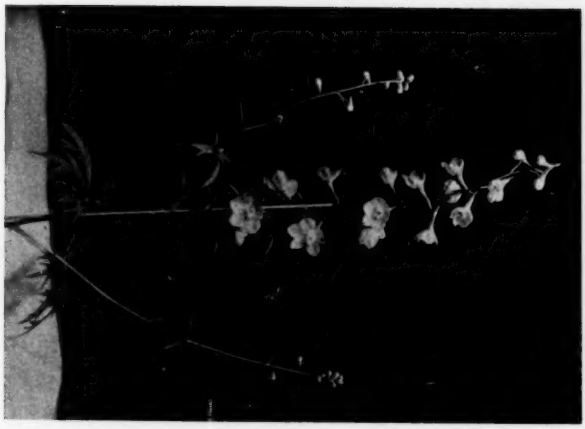
GAGE—DELPHINIUM × BELLADONNA HORT.

Explanation of Plate

PLATE 10

Figs. 1 and 2. Inflorescence and detail of chimaeric derived hexaploid 51-222-7.

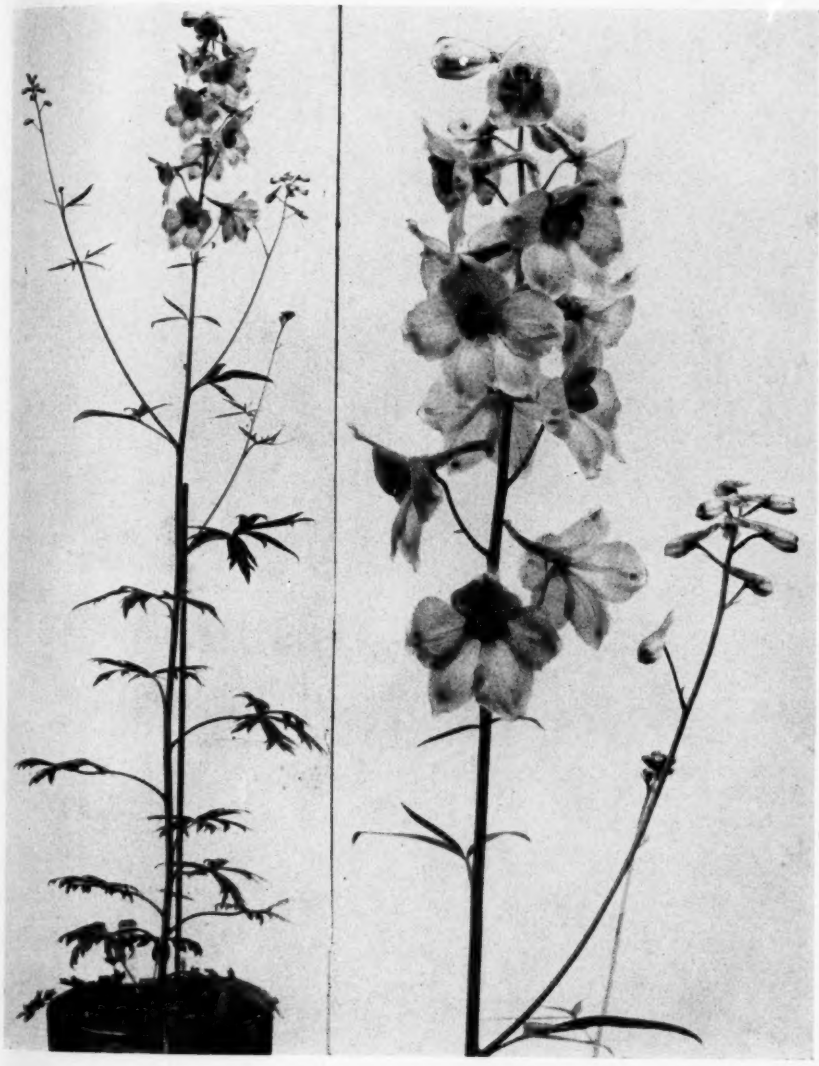
Fig. 3. *Delphinium elatum* L. Plant 47-98-3, seed parent of the 48-27 series of triploids.



Explanation of Plate

PLATE 11

Triploid 48-27-3 (1), habit, (2), detail.



1 2

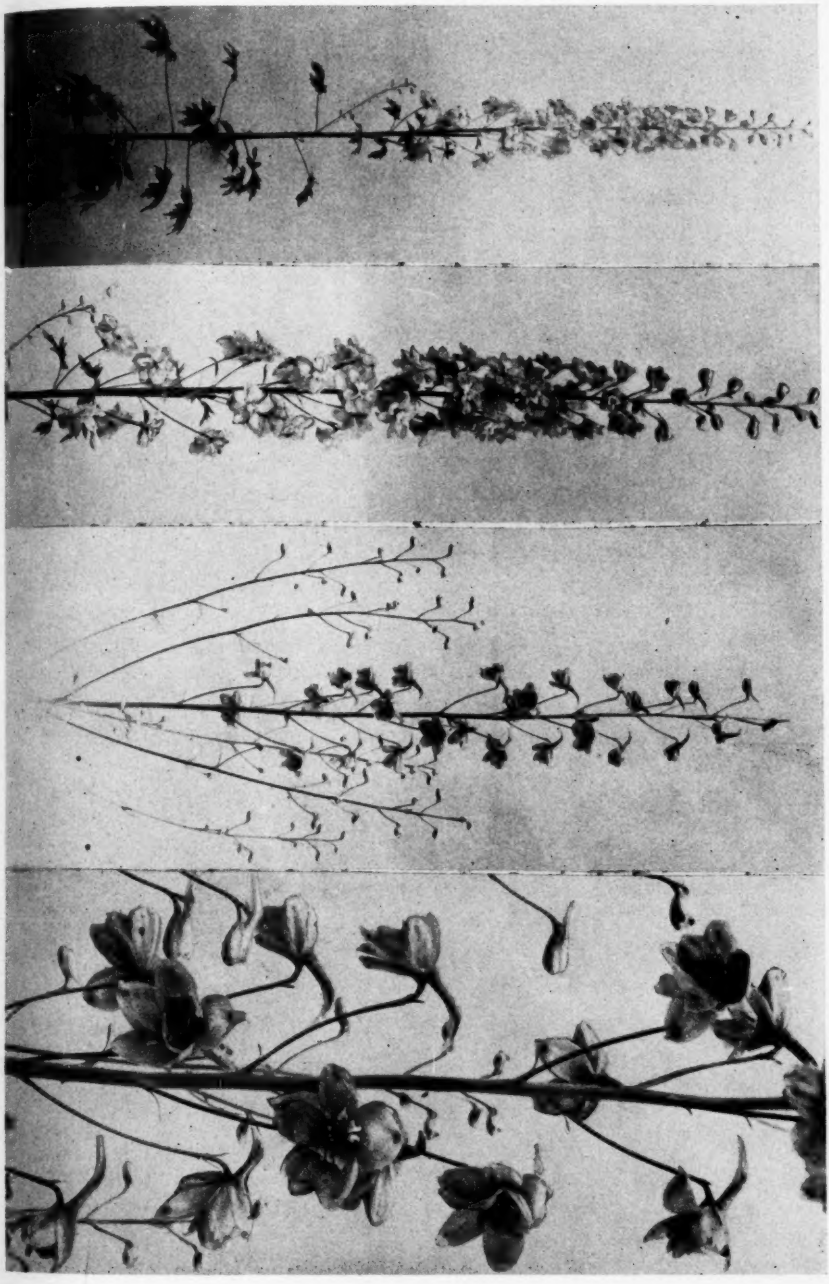
GAGE—DELPHINIUM × BELLADONNA HORT.

Explanation of Plate

PLATE 12

Figs. 1 and 2. Habit and detail of *Delphinium elatum* L., horticultural variety "Summer Skies," seed parent of lines 50-15 and 50-40.

Figs. 3 and 4. Inflorescence and detail of triploid 50-15-4.



1

2 CAGE—DELPHINIUM × BELLADONNA HORT.

4

Explanation of Plate

PLATE 13

Photographs, × 1600; camera-lucida drawings, × 1450.

Fig. 1. Ideogram of the haploid chromosome complement of *D. grandiflorum* var. *chinense*, horticultural form "Blue Butterfly."

Fig. 2. Ideogram of the haploid chromosome complement of *D. cheilanthum*.

Fig. 3. Photograph of somatic metaphase of a white variety of *D. grandiflorum* var. *chinense*, showing satellites on one *C* and two *H*'s.

Fig. 4. Photograph of somatic metaphase of the same plant, showing heterochromatic regions as well as three of the satellites.

Fig. 5. Somatic metaphase of *D. cheilanthum*, showing the four satellited chromosomes.

Fig. 6. Camera-lucida drawing of the cell in fig. 5.

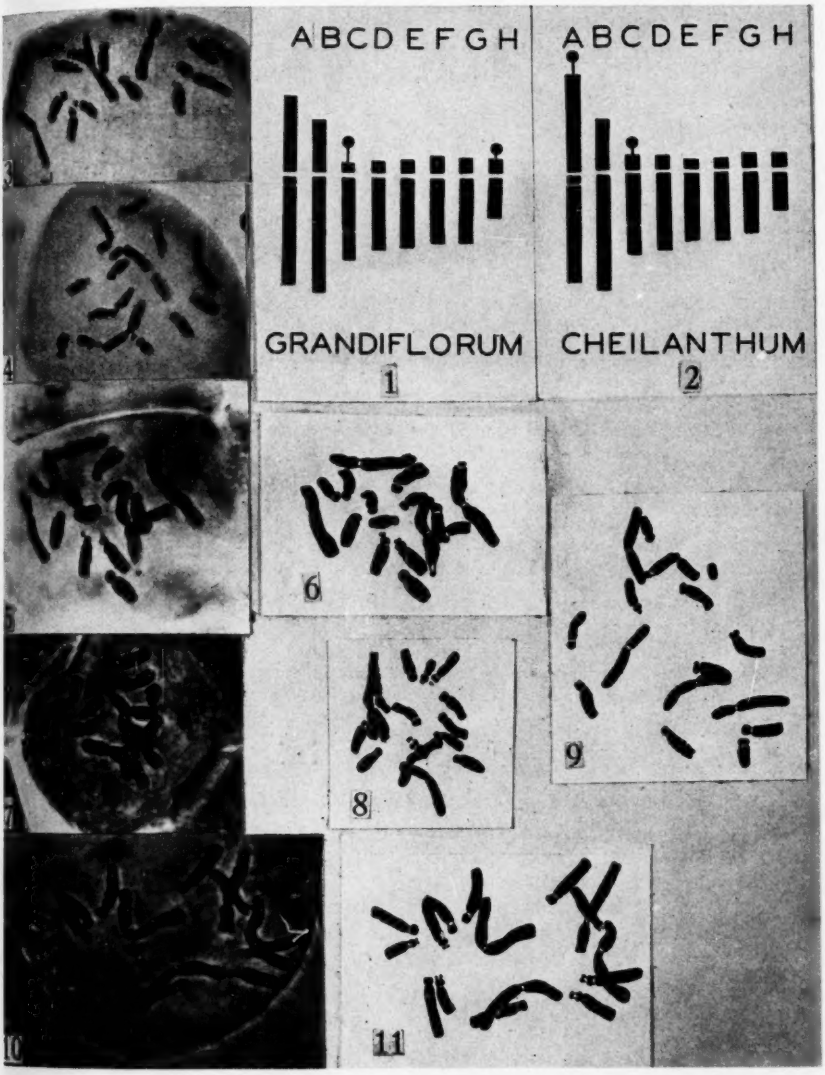
Fig. 7. Photograph of metaphase chromosomes of "Blue Butterfly" from a root-tip preparation.

Fig. 8. Camera-lucida drawing of somatic chromosomes of "Blue Butterfly" showing satellites on both *C*'s and both *H*'s.

Fig. 9. Camera-lucida drawing of somatic metaphase of 47031-1, showing fragment.

Fig. 10. Somatic complement of *D. cardinale* showing satellites on six chromosomes of the diploid complement.

Fig. 11. Drawing of the cell in fig. 10.



GAGE—DELPHINIUM × BELLADONNA HORT.

Explanation of Plate

PLATE 14

Magnification of photographs as indicated; camera-lucida drawings, × 1350.

Fig. 1. Photograph of somatic chromosomes of 48-27-2. × 1500.

Fig. 2. Drawing of the cell in fig. 1.

Fig. 3. Camera-lucida drawing of the chromosomes in a root-tip preparation of 48-6-2, showing satellites on one *A*, three *C*'s, and one *H*.

Fig. 4. Drawing of the somatic chromosomes of "Summer Skies," showing satellites on two *A*'s, two *C*'s, and two *H*'s.

Fig. 5. Camera-lucida drawing of the somatic chromosomes of tetraploid 47-98-3. Satellites visible on two *A*'s, three *C*'s, and two *H*'s.

Fig. 6. Photograph of the cell in fig. 7. × 1500.

Fig. 7. Camera-lucida drawing of MI of triploid 48-27-3, showing 8 II and 8 I.

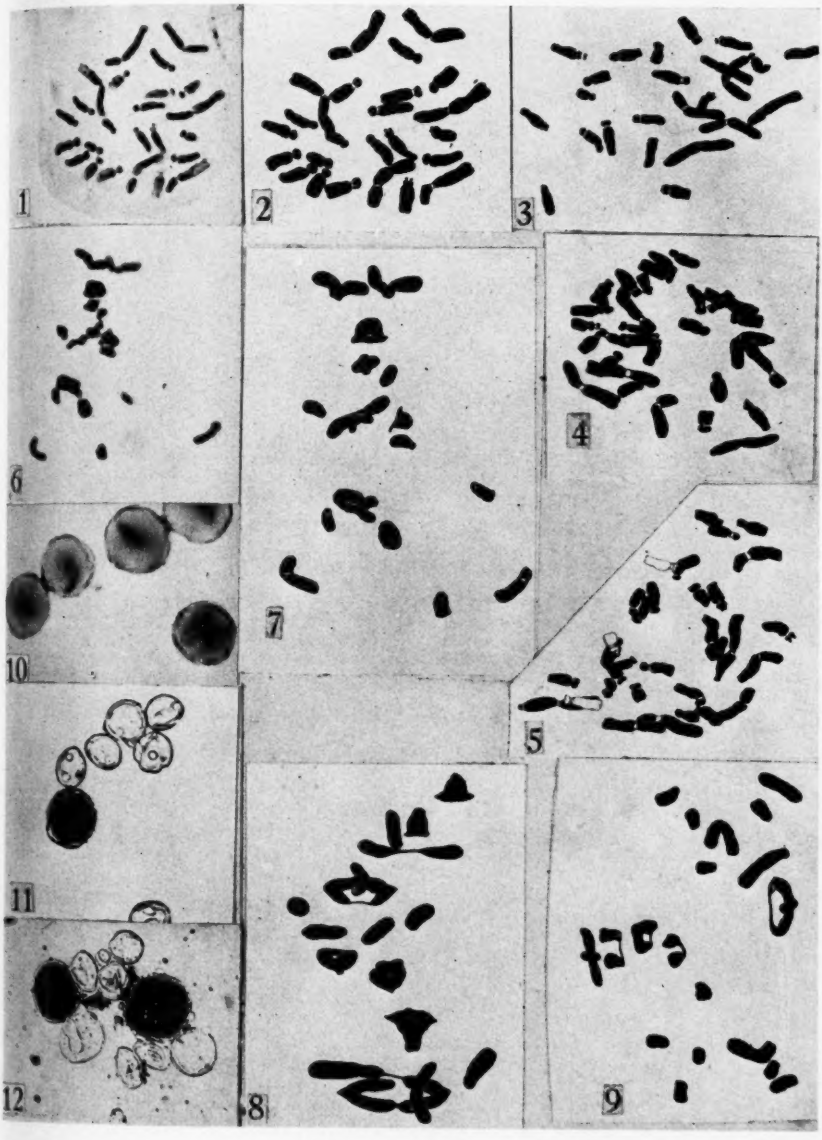
Fig. 8. MI of triploid 48-27-5, showing maximum amount of pairing observed: 1 III, 7 II, and 7 I. Five bivalents of the intermediate chromosomes have two chiasmata.

Fig. 9. MI of triploid 48-27-5, showing greatly reduced pairing: 5 II and 14 I.

Fig. 10. Pollen of "Cliveden Beauty." Pollen mostly viable. × 350.

Fig. 11. Pollen of triploid 48-6-1, showing one unreduced grain. × 350.

Fig. 12. Pollen of 50-20-1, an F_1 between Smith's *Belladonna* and triploid 48-6-2, showing aborted pollen grains. × 350.



GAGE—DELPHINIUM × BELLADONNA HORT.

EXPLANATION OF PLATE

PLATE 15

Photographs, × 1600; camera-lucida drawings, × 1450.

Fig. 1. Diakinesis and early metaphase I of "Blue Butterfly," showing eight II's.

Fig. 2. Photograph of the somatic chromosomes of *D. Belladonna*.

Fig. 3. Anaphase I of 47031-1 with lagging fragment.

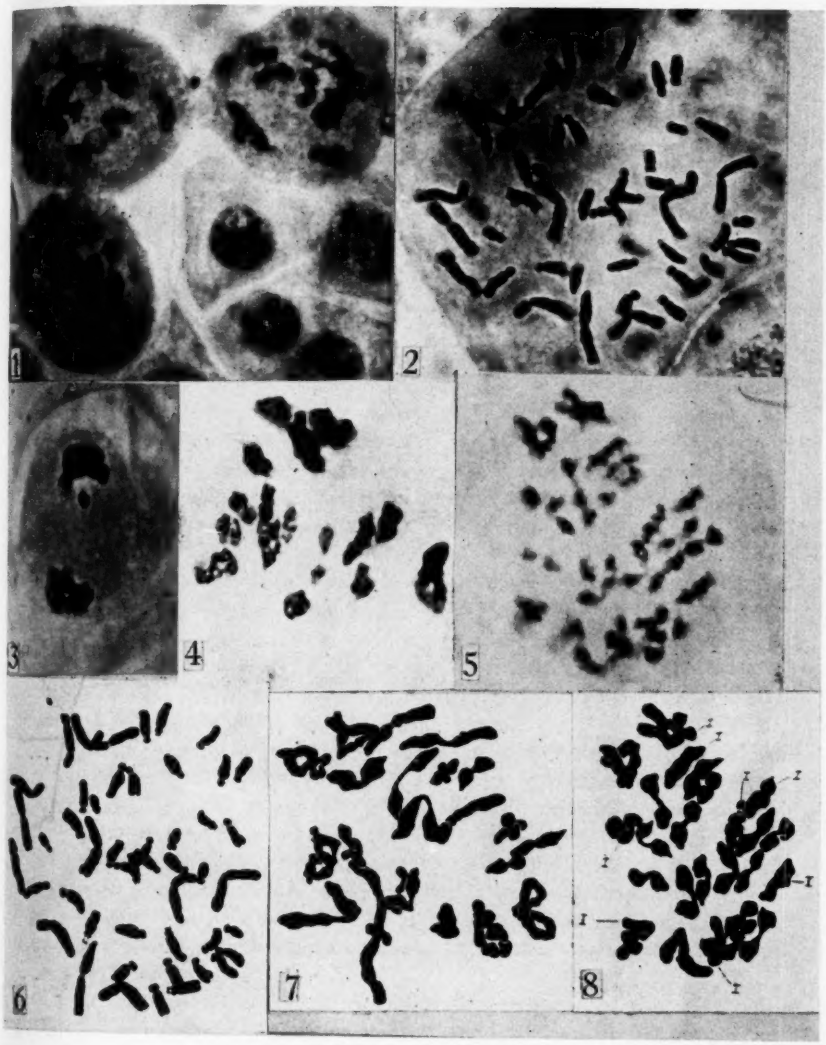
Fig. 4. Diakinesis of "Summer Skies," showing essentially regular pairing.

Fig. 5. Photograph of MI of Smith's *Belladonna*, showing eight univalents and only two of the large bivalents with two chiasmata. This was among the most extreme cases of lack of pairing observed in this plant.

Fig. 6. Drawing of the cell in fig. 2, showing satellites on one *A*, six *C*'s, and one *H*.

Fig. 7. Camera-lucida drawing of diakinesis of Smith's *Belladonna*, showing six univalents.

Fig. 8. Camera-lucida drawing of the cell in fig. 5.



GAGE—DELPHINIUM × BELLADONNA HORT.